THE CAUDAL SKELETON IN LOWER LIASSIC PHOLIDOPHORID FISHES

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THE CAUDAL SKELETON IN LOWER LIASSIC PHOLIDOPHORID FISHES

By COLIN PATTERSON

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SYNOPSIS

The caudal vertebrae and the caudal skeleton and fin are described in *Pholidophorus bechei*, *Pholidolepis* and *Pholidophoropsis*. The centra were formed by calcifications in the sheath of the unconstricted notochord, and were diplospondylous in the middle part of the caudal region. The caudal skeleton is strongly asymmetrical, resembling those of primitive actinopterygians rather than teleosts. The uroneurals of teleosts are modified ural neural arches: the ural neural arches are already considerably modified in pholidophorids. One or two urodermals, relics of the rhombic scales of the caudal axis, persist in a few primitive teleosts. The functional significance of changes in the tail at the pholidophorid/leptolepid transition is discussed, and a new definition of the Teleostei, based on these changes, is proposed.

I. INTRODUCTION

DURING the last few years the caudal skeleton of teleost fishes has been shown to be of great value in tracing relationships between and within major groups. This interest in the caudal skeleton is due primarily to the work of Gosline (1960) who first introduced a rational terminology for the various structures. Nybelin (1963), in a superbly illustrated paper containing the first detailed illustrations of caudal structures in fossil teleosts, gave added precision to the terminology of the tail, and paid particular attention to the nature of the " uroneurals ". Nybelin figured the caudal skeleton in several Jurassic teleost forerunners including *Leptolepis coryphaenoides*, *L. normandica* and *L. dubia*, but the structure of the tail in the ancestors of the leptolepids, the pholidophorids, has so far remained unknown. During a visit to the Royal Scottish Museum, Edinburgh, in October 1966, I came across a specimen from the Lower Lias of Lyme Regis, Dorset, identifiable as *Pholidophorus bechei*, in which the scales are missing, exposing a well preserved caudal endoskeleton. In trying to interpret this specimen I have examined the British Museum (Natural History) collections of Lower Lias pholidophorids, which have recently been revised by Nybelin (1966), and found that the caudal skeleton is occasionally visible or can be prepared in specimens of *Pholidophorus bechei*, *Pholidolepis* and *Pholidophoropsis*. The primary purpose of the descriptions of caudal structures in these fishes which follow is to settle the " uroneural/urodermal " question, but other points in the structure of the caudal skeleton and fin in these pholidophorids throw light on the evolution of teleosts and a discussion of these is added.

My best thanks are due to Prof. Orvar Nybelin, who has been most generous with advice, with unpublished photographs of pholidophorid caudal skeletons and unpublished information on teleost caudal skeletons, and has read the manuscript of this paper. Dr. P. H. Greenwood has also kindly read the paper in manuscript. I am grateful to Drs. C. D. Waterson and R. S. Miles of the Royal Scottish Museum for the loan of a specimen of *Pholidophorus bechei*, and to Mr. P. J. Green, who took the photographs.

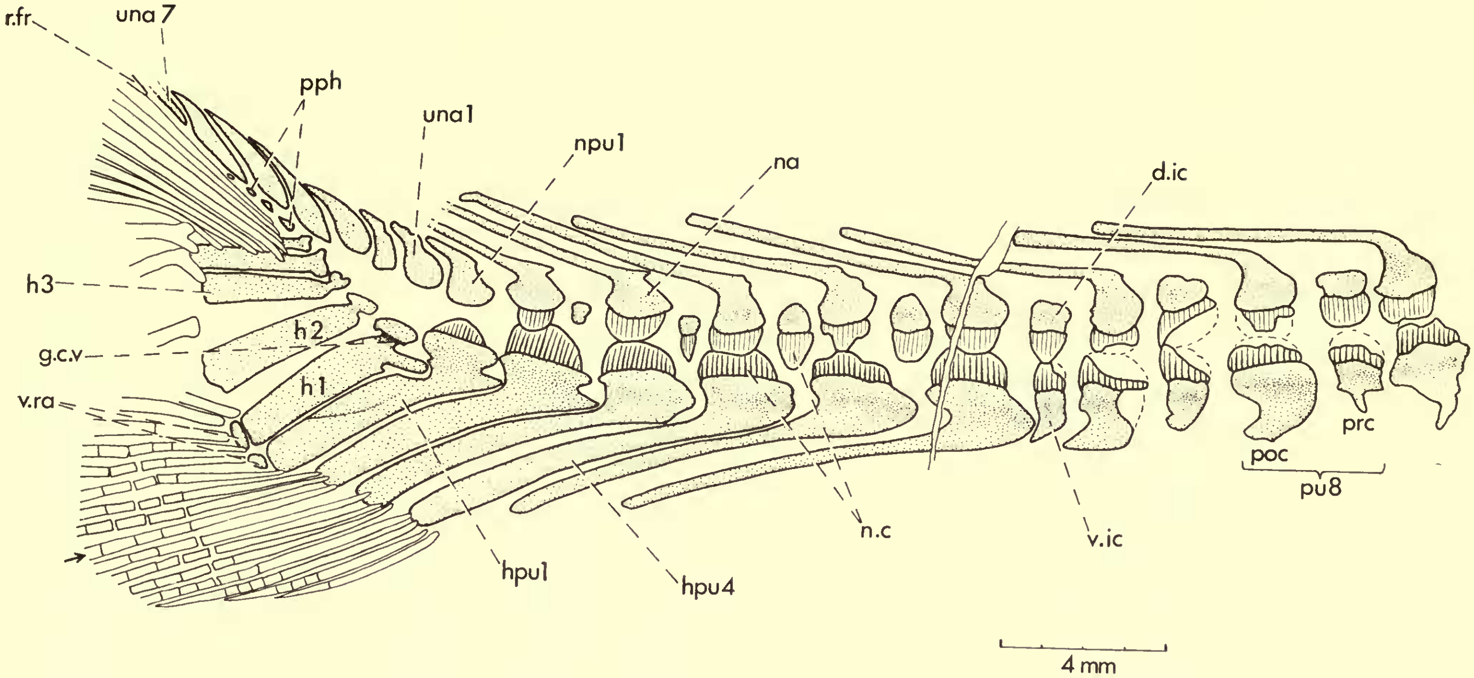
The abbreviation RSM refers to the Royal Scottish Museum, Edinburgh. Specimens referred to by a number without prefix or with the prefix " P " are in the Department of Palaeontology, British Museum (Natural History); the prefix BMNH indicates dried skeletons in the Department of Zoology, British Museum (Natural History).

II. DESCRIPTION

In this section the caudal skeleton is described in three pholidophorids from the Lower Lias of Lyme Regis, Dorset, *Pholidophorus bechei* Agassiz, *Pholidolepis dorsetensis* Nybelin, and *Pholidophoropsis maculata* Nybelin.

Pholidophorus bechei is the type species of the genus. The caudal skeleton is visible in 19010 (Pl. 1, Text-fig. 1: the skull of this specimen was figured by Rayner 1948, fig. 26), RSM 1888.61.73 (Pl. 3, fig. 1; Text-figs 2A, 5A), P.34822 (Text-figs 2B, 5B) and P.48820 (Text-fig. 5C). P.154 (Pl. 5, fig. 1) and several other specimens have also been used in preparing the description.

Pholidolepis dorsetensis Nybelin (1966 : 387) is the only species of a genus set up by Nybelin for Lower Liassic pholidophorids differing from *Pholidophorus* principally in reduction in the enamel covering of the dermal bones, loss of fulcra from all fins except the caudal, and in the presence of thin, cycloid scales. Nybelin suggested that *Pholidolepis* might be intermediate between *Pholidophorus* and *Leptolepis*. The caudal skeleton is partially visible in several specimens of *P. dorsetensis*, the best being P.6067 (Pl. 2; Text-fig. 3), P.44709 (Pl. 3, fig. 2; Text-fig. 4A) and P.939*c* (Text-fig. 4B).



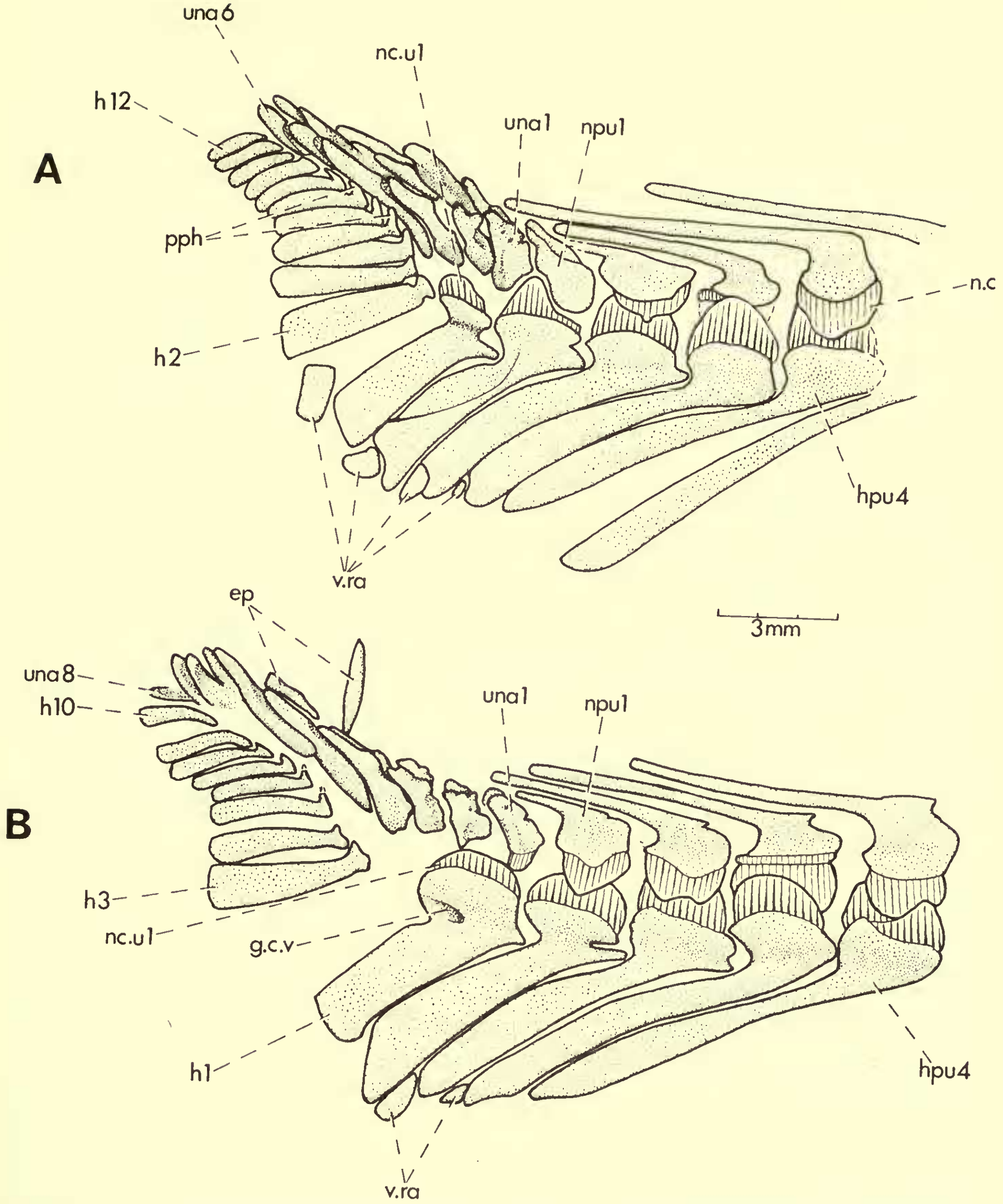
TEXT-FIG. 1. *Pholidophorus bechei* Agassiz. The posterior part of the vertebral column and the base of the caudal fin as preserved in 19010 (see also Pl. 1). *d. ic*, dorsal intercalary; *g.c.v*, groove for caudal vein and artery on first hypural; *h 1–3*, hypurals 1–3; *hpu 1*, *hpu 4*, haemal spines of first and fourth pre-ural vertebrae; *na*, neural arch; *n.c*, notochordal calcifications (hemicentra); *npu 1*, first pre-ural neural arch; *poc*, *prc*, *pu 8*, postcentrum and precentrum of eighth pre-ural vertebra; *pph*, postero-dorsal processes on heads of upper hypurals; *r.fr*, reduced uppermost hypaxial fin-ray; *una 1*, *una 7*, first and seventh ural neural arches; *v.ic*, ventral intercalary; *v.ra*; ventral caudal radials. An arrow marks the lowermost principal caudal ray.

The genus *Pholidophoropsis* Nybelin (1966 : 411) contains Lower Liassic pholidophorids in which the scales are thin and cycloid and the dermal bones with little enamel as in *Pholidolepis*, but which in other respects resemble *Pholidophoroides*. There are two species, *P. caudalis* (Woodward) and *P. maculata* Nybelin. In *P. caudalis* the caudal skeleton is not well exposed in any available specimen, but the caudal squamation is well shown in the holotype, 43055 (Text-fig. 8). The paratype of *P. maculata*, P.7582 (Pl. 4; Text-fig. 6) has the caudal skeleton somewhat disturbed but otherwise well preserved.

(a) *Distinction between ural and pre-ural structures.* Nybelin (1963 : 487) introduced the distinction between pre-ural centra, carrying normal or little modified haemal arches and spines, and ural centra, carrying hypurals. The boundary between these is marked by the point at which the caudal artery and vein, carried within the haemal arches of the pre-ural vertebrae, fork and pass lateral to the hypurals, which do not have a median canal proximally. 19010, *Pholidophorus bechei*, is the only available specimen in which the axial skeleton is preserved in the round. In this specimen (Pl. 1; Text-fig. 1) the exit of the caudal vessels from the haemal canal is marked by a horizontal groove (*g.c.v.*) on the first hypural (*h 1*). Just below this groove on the first hypural there is a peg-like process passing forwards and fitting in a notch on the hind face of the first pre-ural haemal arch (*hpu 1*). The succeeding hypurals are without such a process while the two last haemal arches have a less distinct process. A similar peg-like process can be recognized on the first hypural of *Leptolepis coryphaenoides* and *L. normandica* (Nybelin 1963, text-figs 9, 10), *L. dubia* (Text-fig. 10), *Salmo*, etc., and in pholidophorids it is a useful means of recognizing the first hypural in specimens where the caudal skeleton is too crushed to show the groove for the caudal vessels. In P.34822 (Text-fig. 2B) the groove for the caudal vessels on the first hypural is partially covered, forming a canal anteriorly.

The validity of the ural/pre-ural dividing line as a morphological boundary is supported by the fact that in pholidophorids the pre-ural neural arches are fused with the neural spines into median structures while the ural neural arches are paired (p. 210).

(b) *The vertebral centra.* The vertebral column is best preserved in 19010, *Pholidophorus bechei* (Pl. 1; Text-fig. 1). The notochord was unconstricted. Above and below the space occupied by the notochord there is a series of calcifications in the form of half-rings (*n.c*), normally lying opposite one another in dorso-ventral pairs which meet or almost meet lateral to the notochord. The neural and haemal arches, and in the middle part of the caudal region the independent dorsal and ventral intercalaries (*d.ic, v.ic*; terminology of Schaeffer 1967), are applied to the half-ring calcifications dorso-laterally and ventro-laterally, but do not cover them laterally. As preserved, these calcifications (hemicentra) differ sharply from the endochondral bone of the neural and haemal arches in their dark colour, dense, fibrous texture and vertical striation (Pl. 1). In thin section the hemicentra differ from the trabecular, sparsely cellular bone of the arches in being solid, without cell spaces or vascular canals, and in containing many tangentially arranged fibres, which presumably account for their dark colour and vertically striated appearance.

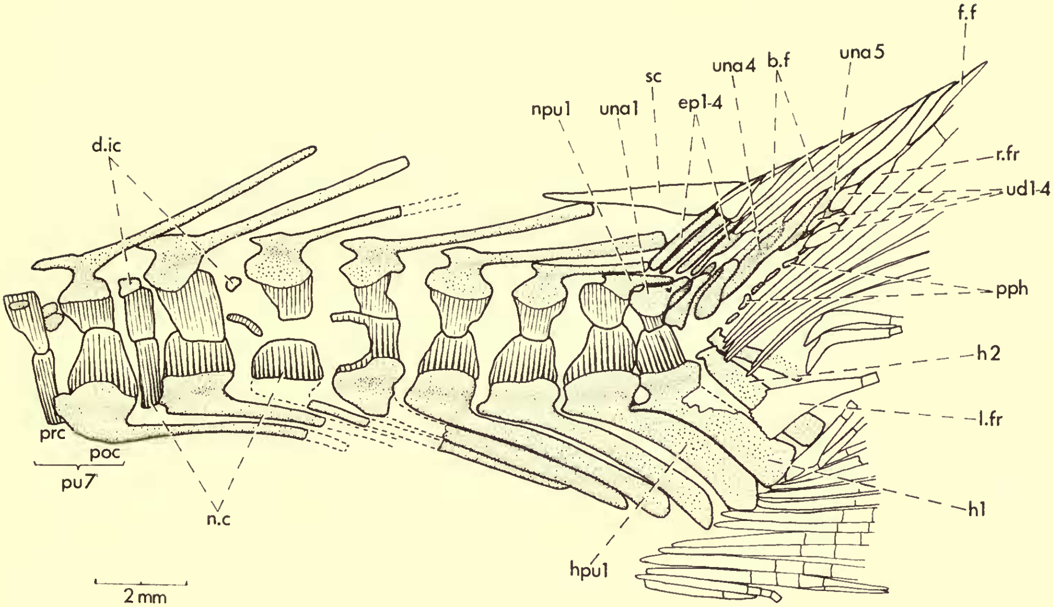


TEXT-FIG. 2. *Pholidophorus bechei* Agassiz. The caudal skeleton as preserved in A, RSM 1888.61.73 (see also Pl. 3, fig. 1); *B*, P.34822. Details of the ural neural arches of these specimens are shown in Text-fig. 5. In *B* the second hypural is missing. *ep*, epurals; *g.c.v*, groove for caudal vessels on first hypural; *h 1*, *h 2*, *h 3*, *h 10*, *h 12*, hypurals 1–12; *hpu 1*, *hpu 4*, first and fourth pre-ural haemal spines; *n.c*, notochordal calcifications (hemicentra); *nc.u 1*, ventral hemicentrum of first ural centrum; *npu 1*, first pre-ural neural arch; *pph*, postero-dorsal processes on heads of upper hypurals; *una 1*, *una 6*, *una 8*, first, sixth and eighth ural neural arches; *v.ra*, ventral caudal radials

In structure these hemicentra agree exactly with the centra of the Triassic pholidopleurid *Australosomus* (Stensiö 1932 : 174, pls 35–37). Stensiö concluded that the ring-like centra of *Australosomus* are chordal, not perichordal as are the centra of most actinopterygians. Nielsen (1949 : 134, pl. 6) found that in one specimen of *Australosomus* the small precentra in the diplospondylous middle part of the caudal region consisted of independent dorsal and ventral half-rings, just as in *P. bechei*. The structure and arrangement of the centra in *P. bechei* shows that, like the centra of *Australosomus*, they are calcifications in the sheath of the notochord: this interpretation is supported by the presence of ring-like calcifications in the sheath of the notochord of larval *Clupea* (Ramanujam 1929 : 377) and by the recent discovery (François 1966 : 292) that in *Salmo* the first calcification of the centrum (in ontogeny) is a median ventral crescentic calcification in the sheath of the notochord. In *Pholidophorus bechei* and in *Pholidophoropsis* the dorsal and ventral hemicentra appear to be separate throughout the vertebral column, but in *Pholidolepis* they tend to fuse with each other to form complete rings (Text-fig. 4A).

In *Pholidophorus bechei*, *Pholidophoropsis* and *Pholidolepis* the vertebral column is diplospondylous in the middle part of the caudal region, as it is in *Australosomus* and many holosteans. In *P. bechei* (Pl. 1; Text-fig. 1) about twelve vertebrae are diplospondylous, the majority of the caudal vertebrae. Passing forwards from the tail, the last complete precentrum (*prc*) (carrying no neural or haemal spine, Schaeffer 1967) lies in front of the sixth pre-ural centrum and in front of this there are about seven more segments in which separate pre- and postcentra (*poc*) are developed. In front of the second to fifth pre-ural centra there are no independent ventral intercalaries or ventral notochordal calcifications, but the dorsal intercalaries remain free, all but the last with a small notochordal calcification. In *Pholidolepis* (Pl. 2; Text-fig. 3), although the vertebral column is never so well preserved as it is in some specimens of *P. bechei*, the number of diplospondylous segments seem to be about the same as in *P. bechei*: 38163 shows complete precentra in front of pre-ural centra 7–15, though other specimens show fewer precentra. In *Pholidophoropsis* there are at least five diplospondylous segments (pre-ural 6–10) in P.7582, *P. maculata*. In these pholidophorids it is impossible to be certain whether the intercalaries fused with the neural and haemal arches or were absent in centra which are not diplospondylous. Appearances in *P. bechei* (Text-fig. 1) and *Pholidolepis* (Text-fig. 3) suggest that the ventral intercalaries fuse with the haemal arch of the centrum behind them, but it is quite possible that intercalaries were absent in monospondylous segments, as they appear to be in teleosts.

In *P. bechei* the last complete centrum, with both dorsal and ventral notochordal calcifications, is the second pre-ural in 19010 (Text-fig. 1), the first pre-ural in RSM 1888.61.73 (Text-fig. 2A) and the first ural in P.34822 (Text-fig. 2B) and other specimens. In 19010 there is only a ventral hemicentrum in the first pre-ural centrum, and in RSM 1888.61.73 there is only a ventral hemicentrum in the first ural centrum, above the first hypural. In all specimens the notochord was uncalcified and unconstricted behind the first hypural, though the close approximation of the heads of the hypurals and the neural arches in the posterior ural region (Text-figs 1, 2) shows that the notochord must have decreased in diameter very sharply.



TEXT-FIG. 3. *Pholidolepis dorsetensis* Nybelin. The posterior part of the vertebral column and the base of the caudal fin as preserved in P.6067 (see also Pl. 2). *b.f.* epaxial basal fulcra; *d.ic*, dorsal intercalaries; *ep 1–4*, epurals; *f.f.*, fringing fulcra; *h 1*, *h 2*, first and second hypurals; *hpu 1*, haemal spine of first pre-ural centrum; *l.fr*, expanded base of lowermost fin-ray in upper caudal lobe; *n.c*, notochordal calcifications (hemicentra); *npu 1*, neural arch of first pre-ural centrum; *poc*, *prc*, *pu 7*, postcentrum and precentrum of seventh pre-ural vertebra; *pph*, postero-dorsal processes on heads of upper hypurals; *r.fr*, reduced uppermost hypaxial fin-ray; *sc*, upper caudal scute; *ud 1–4*, urodermals; *una 1*, *una 4*, *una 5*, first, fourth and fifth ural neural arches.

In *Pholidolepis* the last complete centrum is the first pre-ural in some specimens, but is normally the first ural (Text-figs 3, 4): behind this point the notochord was uncalcified and must have decreased in diameter more sharply than in *P. bechei*, for the gap between the hypurals and the ural neural arches seems normally to be obliterated at the level of the fourth hypural. In *Pholidophoropsis* both *P. caudalis* and *P. maculata* (Text-fig. 6) show a series of small notochordal calcifications extending back into the ural region, in the paratype of *P. maculata* (Text-fig. 6) to the level of the eighth hypural (*nc. u 8*).

(c) *The hypurals and haemal spines.* In *P. bechei* (Pl. 3, fig. 1, Text-figs 1, 2) the last four haemal spines (*hpu 1–4*) are broad, long and in contact wtih their neighbours, and support the foremost caudal fin-rays. The last three haemal spines and the first hypural each bear a small triangular or rhomboid distal element (*v.ra*), increasing in size from front to rear. Three to five similar distal bones or cartilages (presumably homologous with those of *Pholidophorus*) are present in *Acipenser* (Whitehouse 1910, pl. 47, fig. 2; Schmalhausen 1912, pl. 15, fig. 12), *Polyodon*

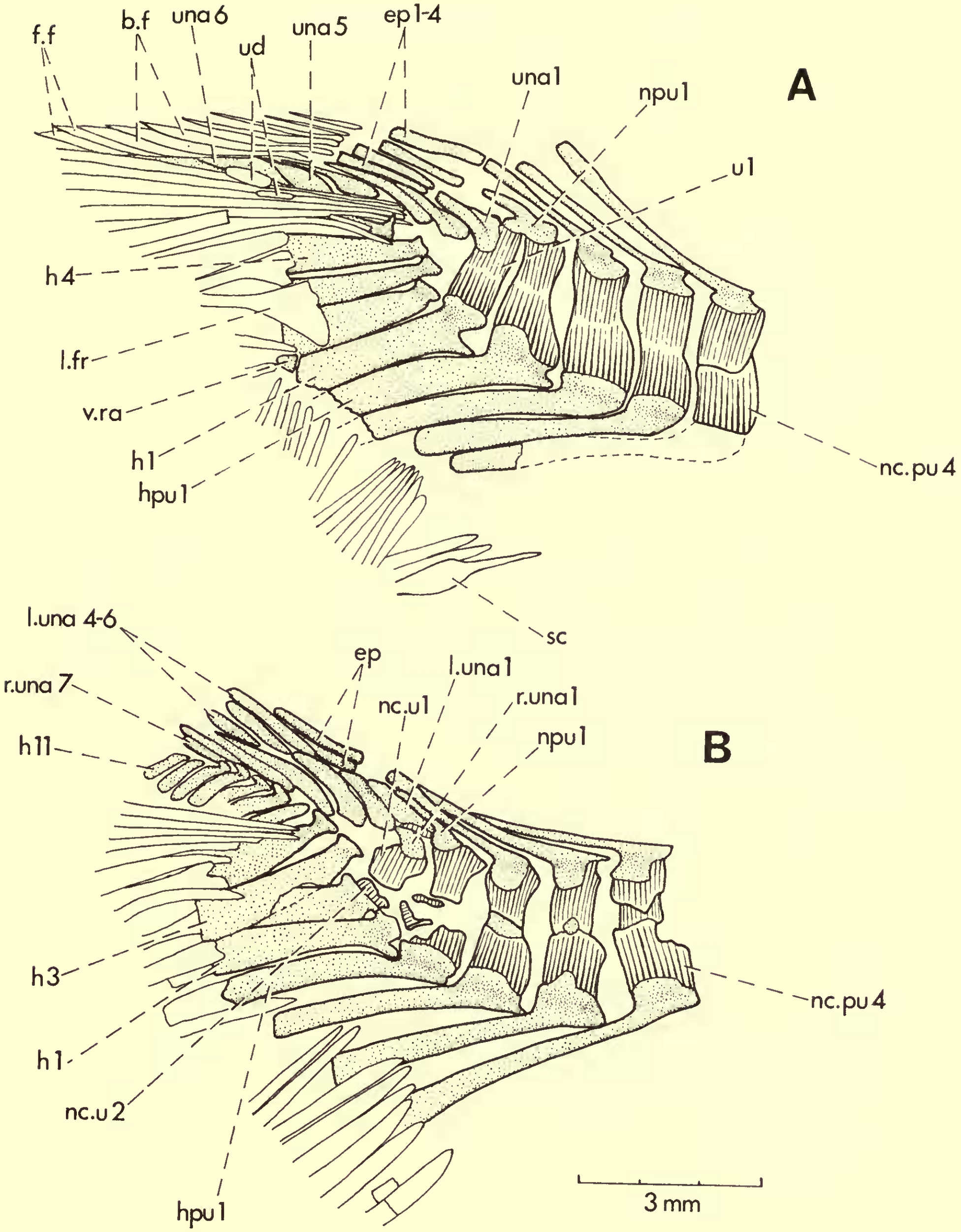
(Whitehouse 1910, pl. 47, fig. 3), *Pteronisculus* (Nielsen 1942, fig. 50) and *Boreosomus* (Nielsen 1942 : 357): they represent the radials of the hypochordal lobe of the fin. There has been considerable argument in the past on the question of the composition of the hypurals in teleosts; whether they contain radial elements or not. In *Pholidophorus*, *Polyodon*, *Pteronisculus* and *Acipenser* the ventral caudal radials are very similar in size, shape and number, and in the ontogeny of *Acipenser* they resemble those of the adult when they first appear (Schmalhausen 1912). Separate or partially separate elements in some teleost embryos have been interpreted as ventral caudal radials (Schmalhausen 1912, Totton 1914), but these do not resemble the ventral radials in *Acipenser* and *Pholidophorus* and are not always present even in primitive teleost embryos. It seems probable that teleosts (see footnote, p. 219) and living holosteans have lost the ventral caudal radials and that the hypurals are not compound structures.

Both in *Pholidolepis* and *Pholidophoropsis* the last four haemal spines are enlarged and support caudal fin-rays, as in *P. bechei*, and at least in *Pholidolepis* (35725, 35562, *v.ra*, Text-fig. 4A) separate hypochordal radial elements were present like those of *P. bechei*.

In *P. bechei*, *Pholidolepis* and *Pholidophoropsis*, as in teleosts, the lower lobe of the forked caudal fin is supported by two hypurals (*h1*, *h2*), the second more slender than the first. In *P. bechei* there are ten upper hypurals (Text-fig. 2A, *h 3–12*), decreasing gradually in length and breadth. In *Pholidolepis* there appear to be only nine upper hypurals (Text-fig. 4B, *h 3–11*). In *Pholidophoropsis* the hypurals are visible only in P.7582, *P. maculata* (Text-fig. 6), where there are nine upper hypurals (*h 3–11*), one less than in *P. bechei*.

In all three genera, but especially in *P. bechei*, the heads of hypurals 4–8 have raised postero-dorsal processes (*p.p.h*) of dense, glossy bone, very like that of the scales and dermal bones in appearance (Pl. 5, fig. 1).

(d) *The neural arches and neural spines.* In *Pholidophorus bechei*, *Pholidolepis* and *Pholidophoropsis* (Text-figs 1–4, 6) the neural spines of the last three pre-ural centra decrease in length progressively so that they all end at approximately the same level, the neural spine of the first pre-ural centrum (*npu 1*) being very short. The neural arches and spines of these last pre-ural centra (best seen in Text-fig. 6, *Pholidophoropsis maculata*, *npu 1*, *npu 2*) are median unpaired structures, in the shape of an inverted " Y ". The succeeding neural arches of the ural region (ural neural arches) are all separate, paired structures, without median neural spines (Text-fig. 5). These paired ural neural arches are rather complex, variable structures. There are up to eight pairs in *Pholidophorus bechei* (*l. una 8*, *r.una 8*, Text-fig. 5) and *Pholidophoropsis* (*una 8*, Text-fig. 6), but the number of ural neural arches is clearly variable since in P.48820 (*P. bechei*, Text-fig. 5C), where the series is complete and well preserved, there are seven on the right side and eight on the left. *Pholidolepis* is not known to have more than seven pairs of ural neural arches (*r.una 7*, Text-fig. 4B). The detailed structure of the ural neural arches is best seen in *Pholidophorus bechei* (Text-fig. 5) but the following description also applies to *Pholidophoropsis* and *Pholidolepis*. The first ural neural arch (*l. una 1*, *r.una 1*,

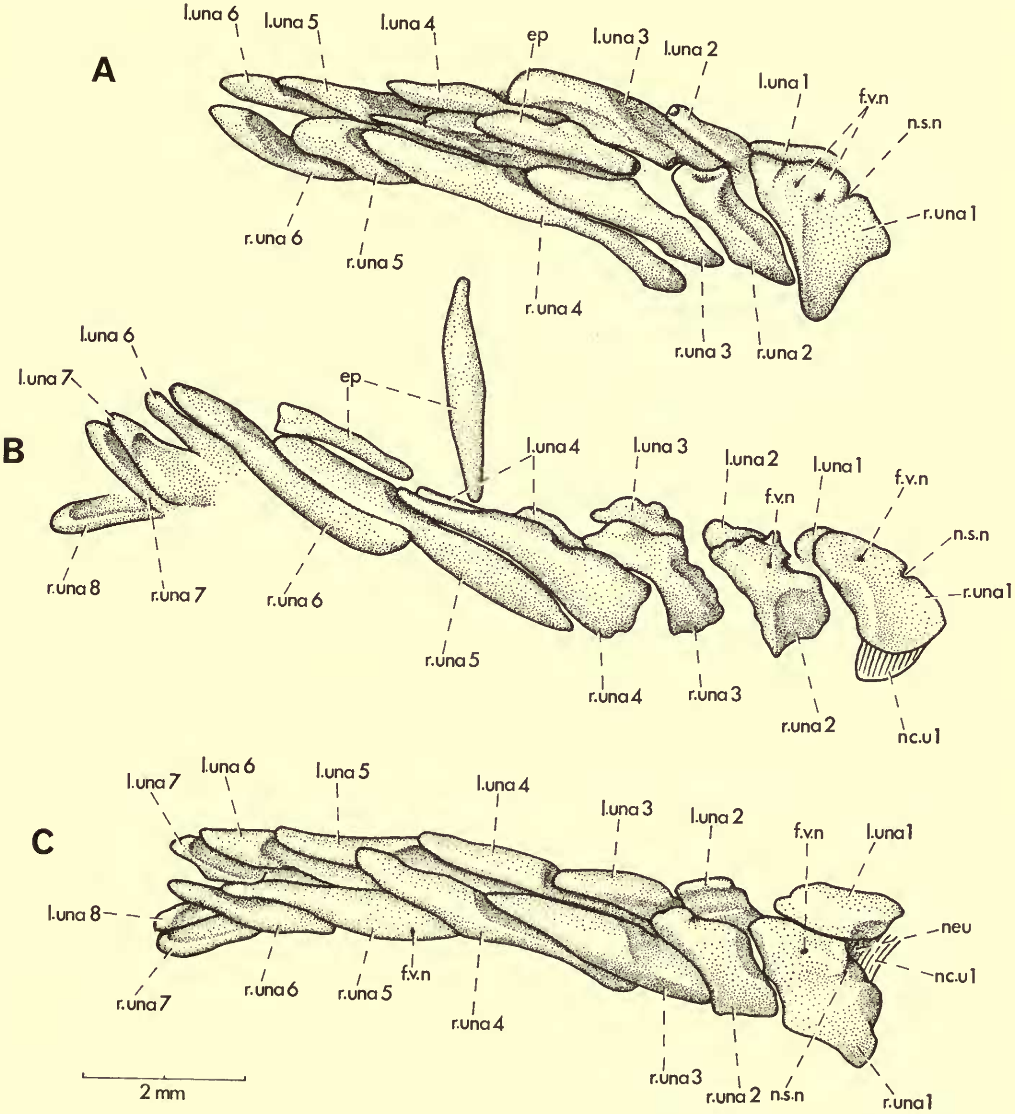


Text-fig. 4. *Pholidolepis dorsetensis* Nybelin. The caudal skeleton as preserved in *A*, P.44709 (see also Pl. 3, fig. 2); *B*, P.939*c*. *b.f*, basal fulcra; *ep 1–4*, epurals, *f.f*, fringing fulcra; *h 1*, *h 3*, *h 4*, *h 11*, hypurals 1–11; *hpu 1*, haemal spine of first pre-ural centrum; *l.fr*, expanded base of lowermost fin-ray of upper caudal lobe; *l.una 1–6*, ural neural arches of left side; *nc.pu 4*, notochordal calcification (hemicentrum) of fourth pre-ural vertebra; *nc.u 1*, *nc.u 2*, notochordal calcifications (hemicentra) of first and second ural centra; *npu 1*, neural arch of first pre-ural vertebra; *sc*, ventral caudal scute; *r.una 1–7*, ural neural arches of right side; *u 1*, first ural centrum; *ud*, urodermals; *una 1–6*, ural neural arches; *v.ra*, ventral caudal radial.

Text-fig. 5; *una 1*, Text-figs 1, 3, 4, 6) corresponds fairly closely with the first pre-ural neural arch (*npu 1*) in shape and size, but is deeper. A notch (*n.s.n*) is usually visible on the anterior margin of the first ural neural arch. This notch corresponds with a notch on the anterior edge of the pre-ural neural arches and must mark the passage of the segmental spinal nerve, or at least of the dorsal root of the nerve. Approximately in the centre of the lateral face of the first ural neural arch, a little above the level of the notch for the spinal nerve, there is usually a small foramen (*f.v.n*, Text-fig. 5B, C, also seen in *Pholidolepis*, Text-fig. 3) which is occasionally double (Text-fig. 5A). Since similar foramina are sometimes present in more posterior ural neural arches (the second in Text-fig. 5B, the fifth in Text-fig. 5C) these foramina are probably vascular and without general significance. The second ural neural arch (*l.una 2*, *r.una 2*, Text-fig. 5) is variable in shape, though always shorter (rostro-caudally) than the first, and is always hollowed antero-laterally to receive the postero-medial surface of the first ural neural arch. Sometimes (Text-fig. 5B, *P. bechei*; Text-fig. 6, *Pholidophoropsis*) the second ural neural arch has an anterior notch for the spinal nerve. In *Pholidolepis* the second ural neural arch is usually produced into a slender postero-dorsal process, curving back above the third arch (Text-fig. 4A). The ural neural arches behind the second are even more variable in shape and are difficult to homologize from one specimen to another. The most important feature of these more posterior ural neural arches is that they are elongated into slender splints, each arch extending back above its successor and forwards below its predecessor. An anterior notch for the spinal nerve is occasionally present on the third ural neural arch (Text-figs 5B, 6) but is never found on more posterior arches. The posterior ural neural arches consist of two regions: the anterior region is hollowed antero-dorsally, receiving the posterior region of the preceding arch in this hollow, while the posterior region is rod-like and fits in the hollow of the succeeding arch. The anterior region of the arch is best developed in the arches in the middle part of the series and extends antero-ventrally around the space occupied in life by the narrow posterior part of the notochord. The rod-like posterior region of the arch is also best developed in the middle part of the series, becoming very short in the last one or two ural neural arches. In *Pholidophorus bechei* the longest of the seven or eight ural neural arches is the fourth (Text-fig. 5A) or the fifth (Text-fig. 5B). In *Pholidolepis* (Text-figs 3, 4) the fourth of the seven ural neural arches is the longest. In *Pholidophoropsis maculata* (Text-fig. 6) the fifth to seventh ural neural arches are equally long. In *P. bechei*, *Pholidolepis* and *Pholidophoropsis*, although the posterior ural neural arches consist internally of cancellous endochondral bone, their exposed lateral surfaces are composed of dense, glossy bone resembling in texture the postero-dorsal processes on the heads of some of the upper hypurals and the scales and fin-rays (Pl. 5, fig. 1).

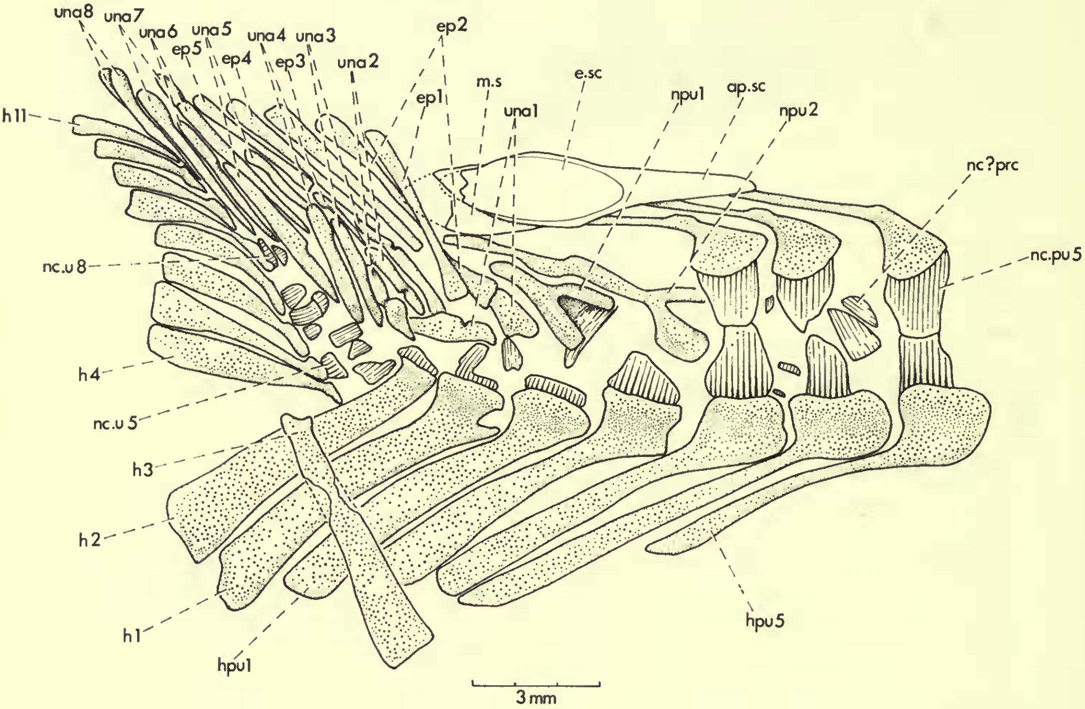
(e) *The epurals*. In teleosts " epural " is the name given to a series of median bones lying behind the last complete neural spine, and supporting epaxial fin-rays. In teleosts the epurals do not seem to exceed three in number except in occasional abnormal individuals. The homologies of the epurals are discussed on p. 220.

In *Pholidophorus bechei* no specimen shows a complete series of epurals well, but in P.154 (Pl. 5, fig. 1) there are three epurals (*ep 1–3*), of which the third is the thickest, above the anterior ural neural arches, and traces of a shorter slender fourth epural (*ep 4*) behind these. The stout third epural and short slender fourth epural of this specimen probably correspond with the two epurals preserved in P.34822



TEXT-FIG. 5. *Pholidophorus bechei* Agassiz. The ural neural arches as preserved in *A*, RSM 1888.61.73; *B*, P.34822; *C*, P.48820. *ep*, epurals; *f.v.n*, foramina, probably vascular, in the ural neural arches; *l.una 1–8*, first—eighth ural neural arches of left side; *nc.u 1*, dorsal notochordal calcification of first ural centrum; *neu*, neural canal; *n.s.n*, notch for spinal nerve on first ural neural arch; *r.una 1–8*, first—eighth ural neural arches of right side.

(*ep*, Text-fig. 5B). In *Pholidolepis* there are four epurals (*ep 1–4*, Text-figs 3, 4A) lying above the first ural and first pre-ural neural arches. In *Pholidophoropsis maculata*, P.7582 shows five long epurals (*ep 1–5*, Text-fig. 6), the first four originating at the tips of the first ural and first pre-ural neural arches, the fifth at the tip of the fourth ural neural arch.



TEXT-FIG. 6. *Pholidophoropsis maculata* Nybelin. The caudal skeleton as preserved in P.7582 (see also Pl. 4). *ap.sc*, anterior process of upper caudal scute; *ep 1–5*, epurals; *e.sc*, enamelled area of upper caudal scute; *h 1*, *h 2*, *h 3*, *h 4*, *h 11*, hypurals 1–11; *hpu 1*, *hpu 5*, haemal spines of first and fifth pre-ural vertebrae; *m.s*, dorsal median scale; *nc ? prc*, notochordal calcification, probably of poorly preserved precentrum; *nc.pu 5*, notochordal calcification (hemicentrum) of fifth pre-ural centrum; *nc.u 5*, *nc.u 8*, notochordal calcifications of fifth and eighth ural centra; *npu 1*, *npu 2*, neural arches of first and second pre-ural vertebrae; *una 1–8*, first to eighth ural neural arches.

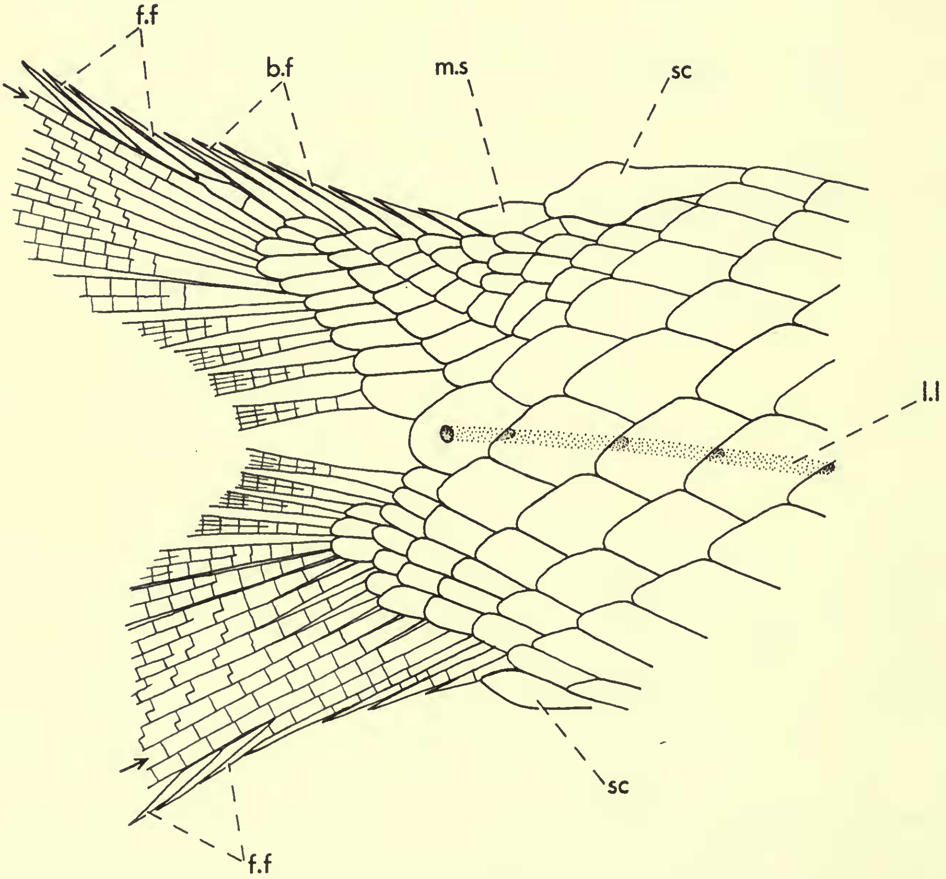
(f) *The fin-rays.* In *Pholidophorus bechei* the caudal fin contains twenty-two to twenty-four principal fin-rays (Text-fig. 7), with the outermost ray in each lobe unbranched and ten or (normally) eleven branched rays in each lobe. Preceding the lowermost principal rays there are six or seven unbranched but segmented rays, grading into fringing fulcra (*f.f*) posteriorly. The uppermost hypaxial fin-ray is much reduced (*r.fr*, Text-figs 1, 7) ending at a notch on the edge of the uppermost principal ray at the level of the first fringing fulcra. This reduced uppermost ray is usually segmented once. The epaxial lobe of the fin is represented only by six or seven basal fulcra (*b.f*), paired, unsegmented structures, grading posteriorly into fringing fulcra (*f.f*) inserted on the upper face of the uppermost principal ray. The seven upper principal rays are very deeply cleft basally, the slender, unsegmented proximal ends crossing the upper hypurals almost at right angles, and ending at the level of the third or fourth hypural (Text-fig. 1; Pl. 1, Pl. 5, fig. 1). The postero-dorsal processes (*p.p.h*) on the heads of the upper hypurals lie against the base of the upper fin-ray. The fin-rays of the lower lobe of the tail are much less deeply cleft and only cover the tips of the lower hypurals and the haemal spines (Text-fig. 1). The proximal end of the innermost ray in each lobe of the fin is expanded, as in *Leptolepis coryphaenoides* and *L. normandica* (Nybelin 1963, figs 9, 10) and various teleosts. The foremost fin-rays in the lower lobe of the fin articulate with the fourth pre-ural haemal spine, and the rays of the lower lobe are equally distributed on the last four haemal spines and the first hypural; the second hypural appears to carry only a single fin-ray, as it does in most teleosts.

In *Pholidolepis* there are twenty to twenty-one principal caudal fin-rays, the outermost in each lobe unbranched, the upper lobe with nine branched rays and the lower with nine or ten: in this *Pholidolepis* is closer than *Pholidophorus* to the primitive teleostean count of nine branched rays in the upper lobe, eight in the lower. In *Pholidolepis*, as in *P. bechei*, there are about six small rays in front of the lower principal rays, the foremost articulating with the fourth pre-ural haemal spine, the seven uppermost hypaxial rays are deeply cleft basally, crossing the upper hypurals and ending on the third hypural (Pl. 2; Text-fig. 3) and the dorsal margin of the fin bears fulcra throughout its length. Nybelin (1966 : 392) was unable to find fulcra on the ventral margin of the tail in *Pholidolepis*, and some specimens, including the holotype, were clearly without them, but in 35725 (paratype), 38163 and P.6067 there are fulcra on the visible parts of the lower edge of the fin. A much reduced uppermost hypaxial fin-ray (*r.fr*, Text-fig. 3) is usually present, as in *Pholidophorus bechei*, but in *Pholidolepis* it is unsegmented. The proximal ends of the innermost fin-rays are expanded, as in *P. bechei*, but in *Pholidolepis* the base of the innermost ray of the upper lobe of the fin, articulating with the third hypural, is much larger than its neighbours (*l.fr*, Text-figs 3, 4A), as in *Leptolepis dubia* (Text-fig. 10) and *Elops* (Nybelin 1963, text-fig. 4).

In *Pholidophoropsis* the number of principal caudal rays is greater than in *Pholidophorus bechei*: in *P. caudalis* there are twenty-five, in *P. maculata* twenty-six to twenty-seven, both species having five small rays in front of the lower principal rays. The two uppermost principal rays are normally unbranched, the lowermost one is often branched. There is no reduced uppermost hypaxial ray such as is present in *P. bechei* and *Pholidolepis*: the unbranched uppermost ray obviously represents this ray in its unreduced condition. The upper hypaxial fin-rays cover the upper hypurals, as in *P. bechei* and *Pholidolepis*. Both margins of the fin carry fulcra throughout their length.

(g) *The squamation.* In *Pholidophorus bechei* the scales are thick, rhombic and enamelled, and scales of this type cover the caudal endoskeleton and the bases of the fin-rays completely (Text-fig. 7). The scaling of the upper lobe of the fin is more extensive than that of the lower, *P. bechei* retaining a vestige of the scaled body lobe of the tail in more primitive actinopterygians. Preceding the basal fulcra (*b.f*) on the upper margin of the fin, which are paired structures, there are two or three median scales (*m.s*), the anterior one (*sc*) scute-like, with a long tapering anterior process (P.3586*e*). On the lower lobe of the fin the small anterior fin-rays are preceded by at least one median scale (*sc*) (38107), probably similar in shape to the scute-like dorsal median scale.

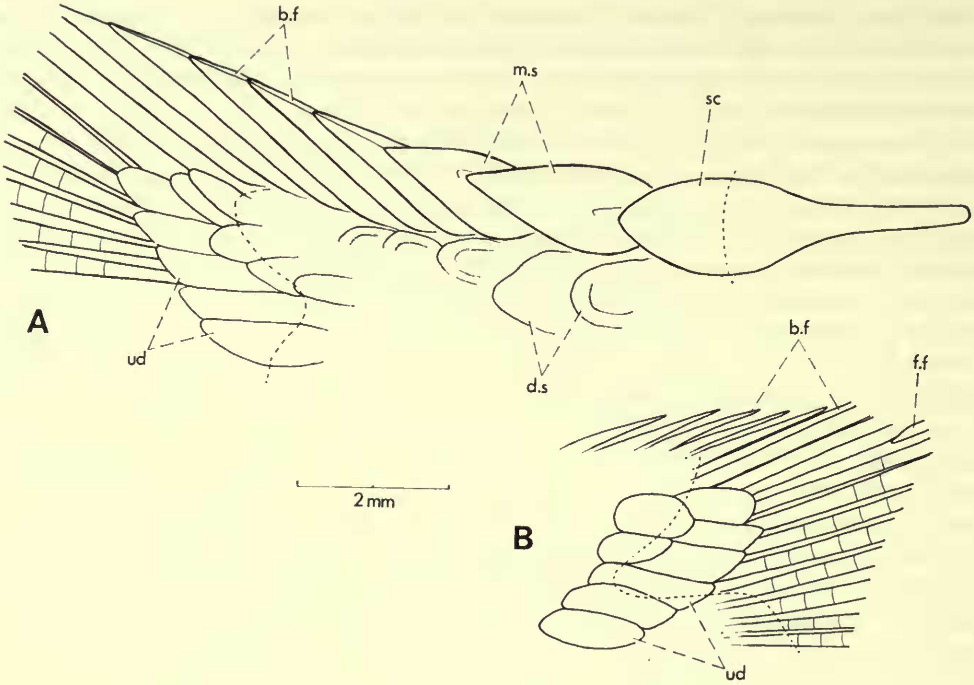
In *Pholidolepis* the trunk scales are thin, cycloid, and without enamel (Nybelin 1966 : 391). In front of the basal fulcra on the upper margin of the caudal fin (*b.f*, Text-fig. 3) there is a thick, median scale with a slender anterior process (29010,



Text-fig. 7. *Pholidophorus bechei* Agassiz. Restoration of the squamation of the caudal region and the base of the caudal fin, based on several specimens. The squamation is drawn as if folded out flat, with the dorsal and ventral median scales shown in surface view. × 3 approx. *b.f*, epaxial basal fulcra; *f.f*, fringing fulcra; *l. l*, course of lateral line; *m.s*, median dorsal scale; *r.fr*, reduced uppermost hypaxial fin-ray; *sc*, upper and lower caudal scutes. Arrows indicate the uppermost and lowermost principal fin-rays.

P.6067 : *sc*, Text-fig. 3), clearly homologous with the similar scale in *Pholidophorus bechei* and in primitive teleosts (Gosline 1965, Patterson, in press). Gosline refers to this median scute-like structure in teleosts as a fulcral scale, but since it is apparently homologous neither with the basal fulcra nor the fringing fulcra it will be referred to here as a caudal scute. Like the urodermals of teleosts (see p. 230) it represents an almost unmodified relic of the thick, rhombic scales of pholidophorids. In *Pholidolepis* the greater part of the caudal scute is covered by thin, cycloid scales, and as in teleosts, it is without enamel. A similar but smaller caudal scute lies in front of the lower caudal lobe in *Pholidolepis* (*sc*, Text-fig. 4A). Lateral to the posterior ural neural arches, in the apex of the wedge-shaped gap between the proximal part of the uppermost hypaxial fin-ray and the epaxial fulcra, there is in *Pholidolepis* a small patch of thick, rhomboid scales. Four of these thick scales are preserved in P.6067 (*ud 1–4*, Text-fig. 3) and P.44707 (*ud*, Pl. 5, fig. 2), three elongated scales lying in an oblique row, overlapping the uppermost one or two hypaxial fin-rays, and a fourth more rounded scale above them. No specimen shows more than four scales clearly, and the preservation is never sufficiently good to show to what extent these thicker scales were covered by thin, cycloid scales. Like the caudal scutes and the fin-rays, these thickened scales are without enamel. In shape and position these scales correspond with the posterior " urodermals " in several of the specimens figured by Nybelin (1963, *Leptolepis normandica*, text-fig. 10, *Ur 7–8*; *Allothrissops*, text-fig. 11, *Ur 8*; " *Thrissops* " text-fig. 12, *Ur 14–15*; *Eurycormus*, text-figs 13, 15, *Ur*).

In *Pholidophoropsis*, as in *Pholidolepis*, the trunk scales are thin, cycloid, and without enamel. Nybelin (1966 : 415) noted that in *P. caudalis* " some of the posteriormost scales are markedly thicker than the body scales ". In both *P. caudalis* and *P. maculata* there is a very thick, conspicuous caudal scute in front of both the upper and lower lobes of the caudal fin, with a slender anterior process (*ap.sc*, Text-figs 6, 8) which evidently passed down into the musculature. The anterior process and the base of the expanded part of this scale (which is covered by thin, cycloid scales) are without enamel, but the exposed part is enamelled (*e.sc*), like the succeeding epaxial fulcra. This enlarged scale is usually followed by a second median scale, also enamelled (*m.s*, Text-fig. 6) and sometimes (Text-fig. 8A) by a third, before the paired fulcra begin. In *Pholidophoropsis* these epaxial fulcra are very large and conspicuous. On the lateral surface of the posterior ural neural arches and the uppermost hypaxial rays, there is a patch of rhombic, thickened and enamelled scales. Normally there appear to be eight of these scales in both *P. caudalis* (Text-fig. 8B) and *P. maculata*, arranged in an oblique row of five, partially covering the bases of the upper hypaxial rays, with three more rounded scales above them. In the holotype of *P. maculata* (*ud*, Text-fig. 8A) there are ten of these scales, an oblique row of five, an oblique row of four antero-dorsal to these, and a single scale above this (this specimen also shows a row of three or four thick, enamelled scales immediately below the thickened dorsal caudal scute, *d.s*, Text-fig. 8A). In both *P. caudalis* and *P. maculata* the greater part of this patch of thick, rhombic scales is covered by thin, cycloid scales, only the tips of the most posterior scales being exposed (Text-fig. 8).



TEXT-FIG. 8. Sketches of the base of the upper lobe of the tail in *A*, 43055, holotype of *Pholidophoropsis maculata* Nybelin, with ten urodermals; *B*, P.3664*a*, *Pholidophoropsis caudalis* (Woodward), with eight urodermals. The broken lines indicate the posterior limit of the thin, cycloid scales. *b.f*, epaxial basal fulcra; *d.s*, dorsal thickened scales in *P. maculata; f.f*, fringing fulcra; *ms*, median dorsal scales between the caudal scute and the basal fulcra; *sc*, caudal scute; *ud*, urodermals.

III. DISCUSSION

(a) *Comparison with chondrosteans, holosteans and teleosts.*

In Lower Liassic pholidophorids, despite the advanced, almost teleostean condition of the skull (Rayner 1948 : 338; Gardiner 1960 : 347) and other such typically teleostean features as intermuscular bones (Lund 1966), the vertebral column and caudal skeleton retain many strikingly pre-teleostean features. In the vertebral column these primitive features include:

1. Formation of the centra entirely by calcifications in the sheath of the unconstricted notochord. Among actinopterygians centra of this type are known only in the Triassic chondrostean family Pholidopleuridae. In teleosts chordal centra occur as a transient phase in larvae of primitive forms such as *Clupea* (Ramanujam 1929) and *Salmo* (François 1966) and in the Upper Jurassic or Lower Cretaceous *Lycoptera*, sometimes classed as a teleost, sometimes as a halecostome, chordal centra appear to have been present in adults (Saito 1936, pl. 4, fig. 5), although the notochordal calcifications are completely covered by perichordal ossifications.

2. Formation of the centra by opposed, partially or completely separate dorsal and ventral hemicentra. Similar centra are known only in parts of the vertebral column of some pholidopleurids, and in the Triassic chondrostean *Turseodus* (Schaeffer 1967).

3. The diplospondylous structure of the vertebrae in the middle part of the caudal region. This is a typically holostean feature: no teleost or leptolepid is known to show diplospondyly of this type, although all the centra are diplospondylous in young individuals of *Lycoptera* (Saito 1936 : 9) and in the Upper Cretaceous " eel " *Enchelion* (Hay 1903 : 441, pl. 37).

In the caudal skeleton the more important primitive features are:

1. The strong asymmetry of the caudal endoskeleton, with a long, upturned axis, despite the almost perfect external symmetry of the fin.
2. The absence of centra or notochordal calcifications beyond the first ural centrum (except for a series of small, irregular calcifications in *Pholidophoropsis*, Text-fig. 6).
3. The presence of free radials at the tips of the last few haemal spines and the first hypural.
4. The numerous hypurals (11–12).
5. The presence of four (*Pholidophorus bechei*, *Pholidolepis*) or five (*Pholidophoropsis*) epurals.

All these features (except the third, the presence of hypaxial caudal radials, which do not seem to have been found yet in holosteans) are typical of chondrosteans and generalized holosteans: none is found in teleosts[1]. Even in the most primitive teleosts (including the leptolepids) the caudal skeleton is almost symmetrical (although the truncated axis is upturned the hind edges of the hypurals form an almost vertical line), there are two (rarely three, Hollister 1936, Greenwood 1967) perichordally ossified ural centra, eight or fewer hypurals and three or fewer epurals. Teleosts appear to have lost the hypaxial radials[1], not incorporated them into the haemal spines and hypurals. But despite the generally archaic structure of the caudal endoskeleton, these pholidophorids approach or foreshadow the teleosts in the presence of only two lower hypurals which support the majority of the principal rays of the lower caudal lobe (in contrast to amioids (Nybelin 1963, text-figs 17–19) and *Eurycormus* (Nybelin 1963, text-figs 13–15)), in the specialization of the ural neural arches (see below, p. 221), the differentiation of the most posterior scales (both median p. 217, and lateral p. 229), and in the reduction of the number of principal caudal fin-rays in the sequence *Pholidophoropsis* (25–27) – *Pholidophorus bechei* (22–24) – *Pholidolepis* (20–21) towards the generalized teleostean arrangement of 19 principal rays with nine branched in the upper lobe, eight in the lower.

In the earliest leptolepids in which the structure of the vertebral column and caudal skeleton are known (*Leptolepis coryphaenoides* and *L. normandica*, Upper Lias, Rayner 1937, Nybelin 1962, 1963) the vertebrae are perichordally ossified cylinders, constricting the notochord, there is no trace of diplospondyly and the caudal skeleton has the generalized teleostean arrangement of two ural centra, three epurals, no hypaxial radials and about eight hypurals whose hind edges are almost vertical (P.7622, *Leptolepis coryphaenoides*, shows six upper hypurals, 37859, *L. dubia*, shows seven). The structure of the caudal skeleton in Lower Liassic pholidophorids shows that in the pholidophorid/leptolepid transition there was a drastic change in the mode of formation of the centra and a sharp reduction in the asymmetry of the caudal endoskeleton. Possible functional explanations of these changes are discussed below (p. 231).

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[1] Nybelin (pers. commn) has found small ossifications and cartilages at the tips of the last three haemal spines and the first hypural in adult Recent *Elops*. These appear to be much reduced ventral caudal radials, and will be described by Nybelin.

(b) *The homologies of the epurals*

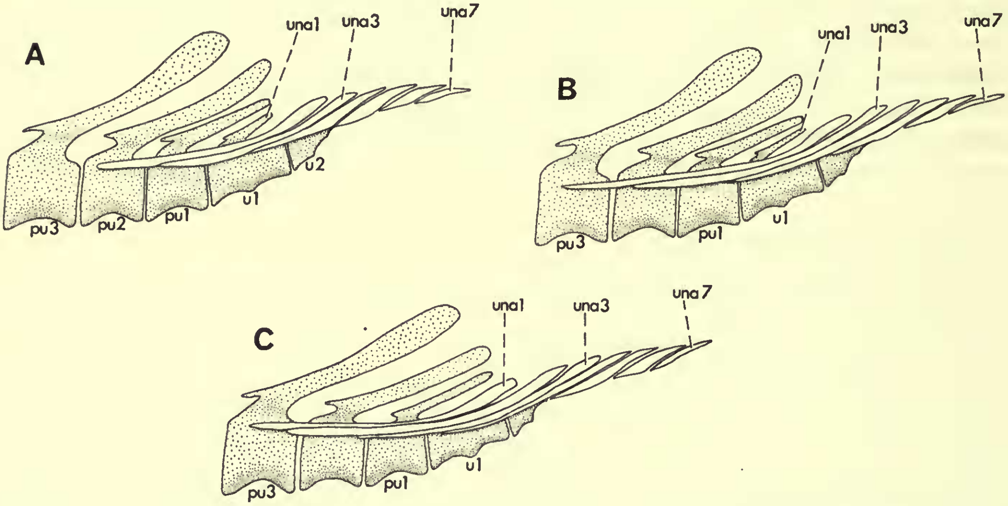
Teleostean epurals, primitively three in number, are normally interpreted as neural spines which have become detached from their neural arches (Gosline 1960, Nybelin 1963, Monod 1967, Greenwood 1967), but they have also been taken to be radials, homologous with the pterygiophores of the dorsal fin (Whitehouse 1910, Goodrich 1930; these authors used the term epural in a different sense from that defined on p. 212). The presence of four epurals in *Pholidophorus bechei* and *Pholidolepis* and five in *Pholidophoropsis* (which is less closely related to the leptolepids and teleosts, p. 236) suggests that the three epurals of generalized teleosts are the remains of a primitively more numerous series. This seems to be confirmed by an examination of more primitive actinopterygians. In the living chondrosteans *Acipenser* (Whitehouse 1910, pl. 47, fig. 2; Schmalhausen 1912, pl. 15, fig. 12) and *Polyodon* (Whitehouse 1910, pl. 47, fig. 3) there is a long series of thirty or more rod-like elements above the posterior neural arches, supporting the epaxial basal fulcra. These cartilages, which are always interpreted as dorsal caudal radials, do not correspond in number or position with the neural arches below them. The only palaeoniscoid in which the caudal skeleton is well known is the Triassic *Pteronisculus* (Nielsen 1942, pl. 24, text-fig. 50), in which there are about fifteen similar elements, also interpreted by Nielsen as dorsal caudal radials, which here have a one-to-one relation to the underlying neural arches. In the Triassic pholidopleurid *Australosomus* (Nielsen 1949, text-fig. 45) there are five dorsal elements, one-to-one above the neural arches. In *Amia* there are three or four dorsal radials (Nybelin 1963, text-fig. 16; Schmalhausen 1912, pl. 18, fig. 56) and in the more primitive amioid *Urocles* there are five (Nybelin 1963, text-fig. 17), in both genera corresponding with the neural arches. Thus there is clear evidence in actinopterygians of a progressive reduction in the number of median dorsal elements below the epaxial basal fulcra (in chondrosteans and most holosteans) or fin-rays (in most teleosts). The epurals of teleosts must be regarded as members of this series of bones, and the name " epural " is sufficiently well established, terse and descriptive to apply to the series in all actinopterygians. There is one-to-one correspondence between the epurals and the neural arches in all the actinopterygians mentioned except *Acipenser* and *Polyodon*: conditions in these two fishes and the fact that in most actinopterygians fulcra or fin-rays articulate with the epurals might suggest that the epurals are dorsal caudal radials, serial homologues of the dorsal pterygiophores, which are primitively not metameric (Lindsey 1956, François 1959). But the articulation between the epurals and the epaxial fulcra or fin-rays is very different from the complex, mobile, muscular joint between dorsal pterygiophores and fin-rays, and in teleosts epaxial fin-rays often articulate with neural spines anterior to the epurals. On the other hand, there is good evidence from several different teleosts that the foremost epural can arise by detachment of a neural spine or can fuse with a neural arch so that it is indistinguishable from a neural spine (Whitehouse 1910, Norden 1961, Patterson, in press, *etc.*): this and the general occurrence, even in palaeoniscoids, of a one-to-one relationship between the epurals and the neural arches indicate that the epurals are detached neural spines, serial homologues of the metameric supraneurals above the anterior neural arches in chondrosteans, most holosteans and many generalized teleosts, which are detached neural spines (Goodrich 1930 : 88; Eaton 1945). If this interpretation is correct, the imperfect correspondence between the epurals and the neural arches in living chondrosteans must be secondary, a reasonable assumption in view of the aberrant nature of the skeleton of these fishes. One is led to the conclusion that the epurals of teleosts are the remains of a longer series of metameric bones in primitive actinopterygians which are detached neural spines, serial homologues of the supraneurals developed anteriorly.

(c) *Uroneurals and urodermals*

On the dorso-lateral surfaces of the ural centra and the first one to four pre-ural centra of primitive teleosts there is a series of paired, elongate bones, extending back between the proximal ends of the epaxial fin-rays. Tate Regan (1910*a*, *b*) named these bones " uroneurals " and interpreted them as " neural arches pertaining to posterior centra which have aborted " (1910*b* : 533). Nybelin (1963) showed that in Upper Jurassic teleosts these bones may be numerous and may extend beyond the axial skeleton on to the surface of the dermal fin-rays, an unlikely position in which to find endoskeletal neural arches. Nybelin compared the series of bones with the elongate rhombic scales covering the body lobe of the heterocercal tail in chondrostean fishes such as *Acipenser*, *Polyodon*, *Birgeria* and *Tarassius*, and interpreted them as scales which have sunk inwards (in phylogeny) and become associated with the vertebral centra, proposing the name " urodermals " for them. The details of the structure of the ural neural arches and the caudal squamation in the pholidophorids described here show that these two interpretations, the endoskeletal " uroneurals " of Tate Regan and the dermal " urodermals " of Nybelin, are not mutually exclusive. The foremost members of the uroneural/urodermal series, normally applied to or fused with the ural and pre-ural centra (the only ones present in the great majority of teleosts), are modified ural neural arches, correctly called uroneurals and referred to as such in the discussion of post-Jurassic teleosts below. The most posterior members of the series, present only in a few primitive teleosts and lying on the uppermost hypaxial fin-rays, are scales, almost unmodified relics of the thick, rhombic scales of *Pholidophorus*, and are correctly called urodermals.

(i) *The uroneurals.*

In *Pholidophorus bechei* (Pl. 1, Pl. 3, fig. 1, Pl. 5, fig. 1; Text-figs 1, 2, 5), *Pholidolepis* (Pl. 2, Pl. 3, fig. 2; Text-figs 3, 4) and *Pholidophoropsis* (Pl. 4; Text-fig. 6) the ural neural arches are paired structures and those behind the first are successively modified into elongate, rod-like structures, each fitting closely into a hollow on the antero-dorsal surface of its successor. In *Pholidophorus bechei* there are seven or eight pairs of ural neural arches, in *Pholidophoropsis maculata* there are eight, and in both species all but the first two pairs are modified, elongate structures. In *Pholidolepis* only seven pairs of ural neural arches have been seen, all but the first pair modified. Since these bones are in series with and grade into the pre-ural neural arches, lie directly over the space occupied in life by the notochord, are thick and consist internally of cancellous endochondral bone, and in *P. bechei* are completely covered by thick, enamelled scales, there can be no doubt that they are endoskeletal neural arches, not dermal scales.



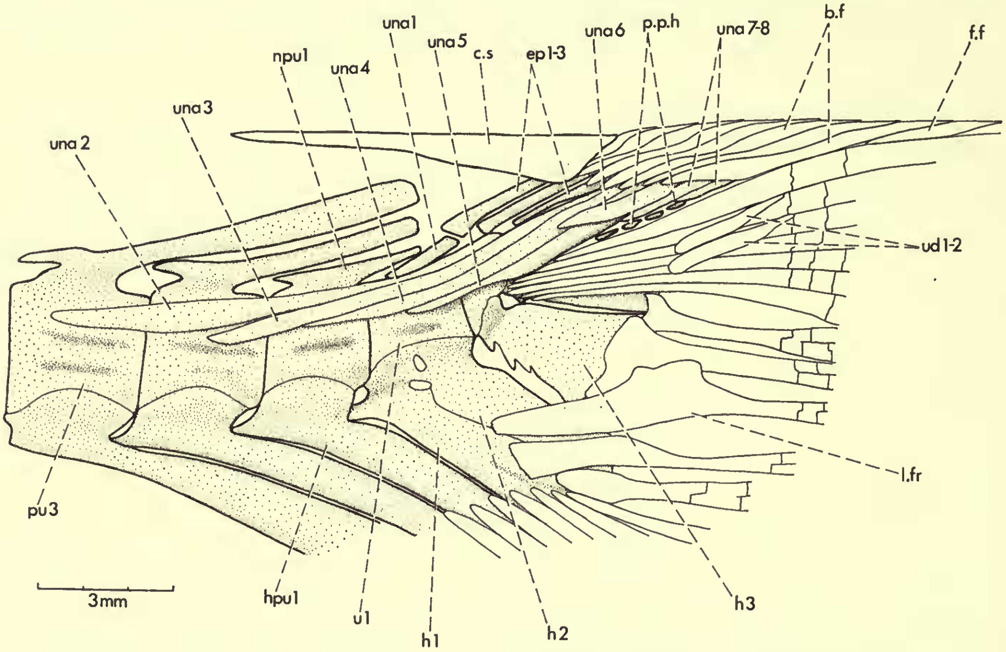
Text-fig. 9. Sketches illustrating variations in the ural neural arches in *Leptolepis coryphaenoides*. In *A* and *B* the first ural neural arch is unmodified, in *C* it is modified into a uroneural. In *A* the first uroneural extends to the second pre-ural centrum, in *B* to the third. *pu 1–3*, pre-ural centra; *u 1*, *u 2*, ural centra; *una 1*, *una 3*, *una 7*, ural neural arches 1–7.

The seven or eight ural neural arches of Lower Liassic pholidophorids may be compared directly with the uroneurals of the Upper Liassic *Leptolepis coryphaenoides* and *L. normandica* (Text-fig. 9; Nybelin 1963, text-figs 9, 10). In P.948 (*L. coryphaenoides*, Nybelin 1963, text-fig. 9) the first ural neural arch is unmodified, as in pholidophorids, and there are six modified ural neural arches (*una 2–7*, Text-fig. 9; *Ur 2–7* in Nybelin's figure). *Ur 8*, the most posterior element labelled in Nybelin's figure, is probably not a ural neural arch but the remnant of the uppermost hypaxial fin-ray, already much reduced in *Pholidophorus* and *Pholidolepis* (*r.fr*, Text-figs 1, 3, 7). In contrast to *Pholidolepis*, where the fourth ural neural arch is the longest and none of the ural neural arches extends forwards beyond the first ural centrum, in *L. coryphaenoides* the second to fourth ural neural arches are equally long, the second extending forwards to the second (Text-fig. 9A) or third (32456, Text-fig. 9B) pre-ural centrum, the third to the first or second pre-ural centrum, and the fourth to the first ural centrum (which in *Leptolepis* and all teleosts supports the first two hypurals and is the product of fusion of two centra). A further variation found in both *L. coryphaenoides* (32467, Text-fig. 9C) and *L. normandica* (32583) is that the first ural neural arch, unmodified in pholidophorids and in most specimens of these two species, is elongated like its successors, extending forwards to the third pre-ural centrum. *Leptolepis normandica* does not seem to differ from *L. coryphaenoides* in the structure of the ural neural arches, but some of the specimens identified as *L. coryphaenoides* may be *L. normandica* since the two species are at present distinguishable only when the head is well preserved.

In the more advanced Upper Jurassic form *Allothrissops* (P.915, P.917*a*, P.3680*c*, P.7663; Nybelin 1963, text-fig. 11, Patterson 1967, text-fig. 3) one can recognize seven ural neural arches, the first unmodified, the second to seventh all greatly elongated and sometimes showing fusions (Patterson 1967, text-fig. 3, D 5+6) or apparent subdivisions (Nybelin 1963, text-fig. 11, *Ur 6–7*). As in some specimens of *Leptolepis coryphaenoides*, the second ural neural arch extends forwards to the third pre-ural centrum, but in contrast to *L. coryphaenoides* the third, fourth, and often the fifth extend to the second pre-ural centrum, the sixth extends to the first pre-ural centrum and the seventh to the first ural centrum. In the related Upper Jurassic *Thrissops* (P.3684; Nybelin 1963, text-fig. 12) the ural neural arches are as in *Allothrissops* except that the second is even more elongate, extending forwards to the fourth pre-ural centrum, and in Nybelin's figured specimen there are seven elongate ural neural arches (*Ur 1–7*).

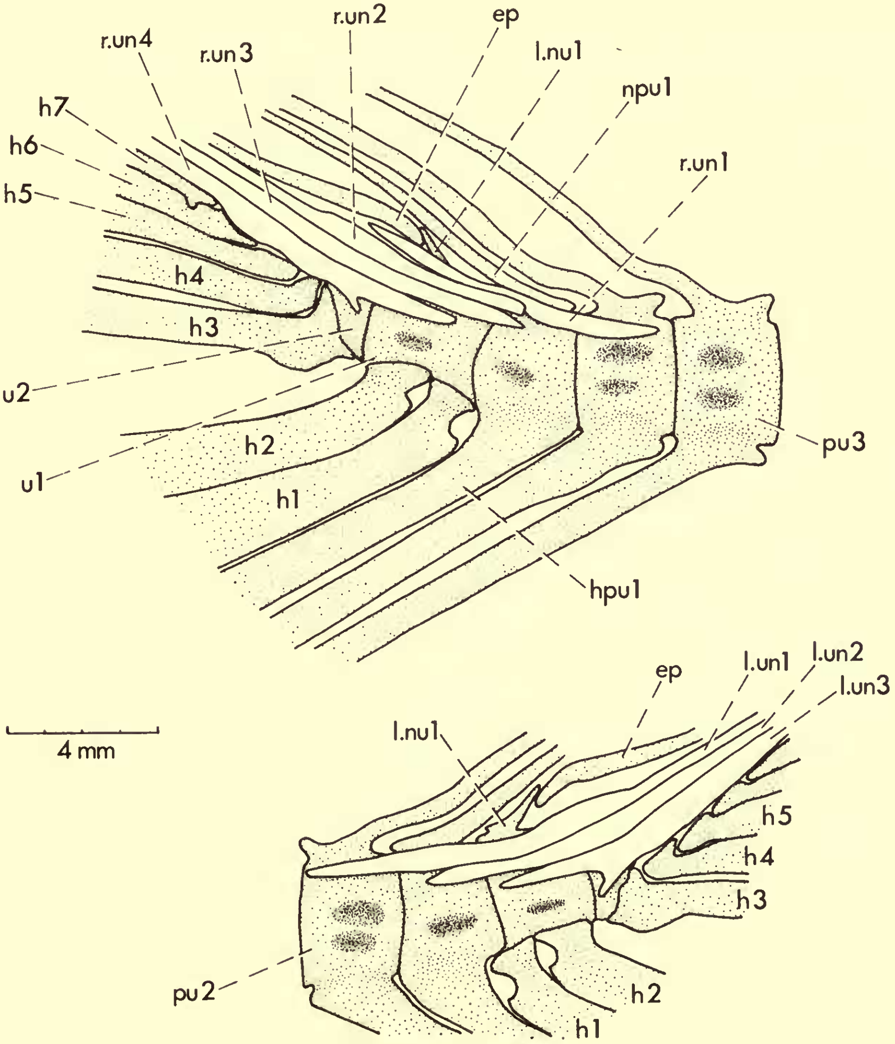
In the Upper Jurassic *Leptolepis dubia* (Text-fig. 10; Nybelin 1963, text-fig. 8, Patterson 1967, text-fig. 6), in which the skull is in many ways more primitive than in *Allothrissops* (Patterson 1967, text-figs 2, 4), the condition of the ural neural arches is more complex. The first five ural neural arches do not differ from those of *Allothrissops* and *Leptolepis coryphaenoides*; the first (*una 1*) is unmodified and the second to fifth (*una 2–5*) are greatly elongated, the second extending forwards to the third pre-ural centrum (*pu 3*). Behind the fifth ural neural arch there are three less elongate bones (*una 6–8*), the first originating well behind the second ural centrum, which are inclined in sequence behind one another as are the preceding ural neural arches, but which lie *lateral* to the fifth ural neural arch. This arrangement can be seen in several specimens (37090, 37847, 37859, 37865; Nybelin 1963, text-fig. 8, *Ur 5–7*, Patterson 1967, text-fig. 6, *D 5–7*) and seems to be constant for the species. In shape and in their mode of articulation with each other (best seen in 37090) these three posterior bones resemble the posterior ural neural arches of pholidophorids and *Leptolepis coryphaenoides*, and like them they end posteriorly *medial* to the bases of the epaxial basal fulcra (*b.f.*). Since these three bones correspond in number and position with the sixth to eighth ural neural arches in pholidophorids they are clearly ural neural arches, despite their differentiation from the more anterior arches and their position lateral to the fifth.

Among known Cretaceous and later teleosts the maximum number of elongate, strap-shaped uroneurals (ural neural arches) is five, which occurs in some specimens of the Upper Cretaceous genera *Xiphactinus*, *Ichthyodectes* and *Gillicus* (Cavender 1966): in some specimens of *Xiphactinus* there are four long uroneurals on one side, five on the other (Cavender 1966 : 6). These Cretaceous ichthyodectids also show the maximum forward extension of the uroneurals, which may reach the fourth pre-ural centrum, as in *Thrissops*. Among living teleosts the maximum number of elongate uroneurals is four, found in some specimens of *Hiodon* (Gosline 1960 : 341). The specimen of *Hiodon alosoides* figured by Gosline (BMNH 1892.12.30.555; 1960, text-fig. 4) shows a most interesting condition. On the left side of the tail (Text-fig. 11) there are three long uroneurals (*l.un 1–3*), the first ending anteriorly on the second pre-ural centrum (*pu 2*), the second and third on the first pre-ural and first ural centra respectively. The third uroneural has a small ventral process on the second ural centrum (*u 2*): this process (present on both sides of the specimen) probably indicates that the third uroneural is a compound structure formed by fusion of two ural neural arches, almost certainly homologous with the fourth and fifth ural neural arches of *Leptolepis*. On the right side of this specimen of *Hiodon alosoides* (Text-fig. 11) there are four uroneurals, as Gosline (1960 : 341) noted, but the first of these (*r.un 1*), ending anteriorly on the second pre-ural centrum, is short



TEXT-FIG. 10. The caudal skeleton of *Leptolepis dubia*, drawn mainly from P.927, slightly restored. *b.f*, epaxial basal fulcra; *c.s*, caudal scute; *ep 1–3*, epurals; *f.f*, fringing fulcra; *h 1–3*, hypurals 1–3; *hpu 1*, first pre-ural haemal spine; *l.fr*, expanded base of lowermost fin-ray of upper caudal lobe; *npu 1*, first pre-ural neural arch; *p.p.h*, postero-dorsal processes on heads of upper hypurals; *pu 3*, third pre-ural centrum; *u 1*, first ural centrum; *ud 1–2*, urodermals; *una 1–8*, first–eighth ural neural arches.

and is continuous posteriorly with the small neural arch on the first ural centrum (the first ural neural arch), a structure which is unmodified on the left side of the specimen (*l.nu 1*), and in all the fishes so far discussed except some individuals of *Leptolepis coryphaenoides* and *L. normandica* (Text-fig. 9C). The second uroneural (*r.un 2*), the antimere of the first on the left side of the fish and representing the second ural neural arch, is truncated anteriorly and ends on the first pre-ural centrum,



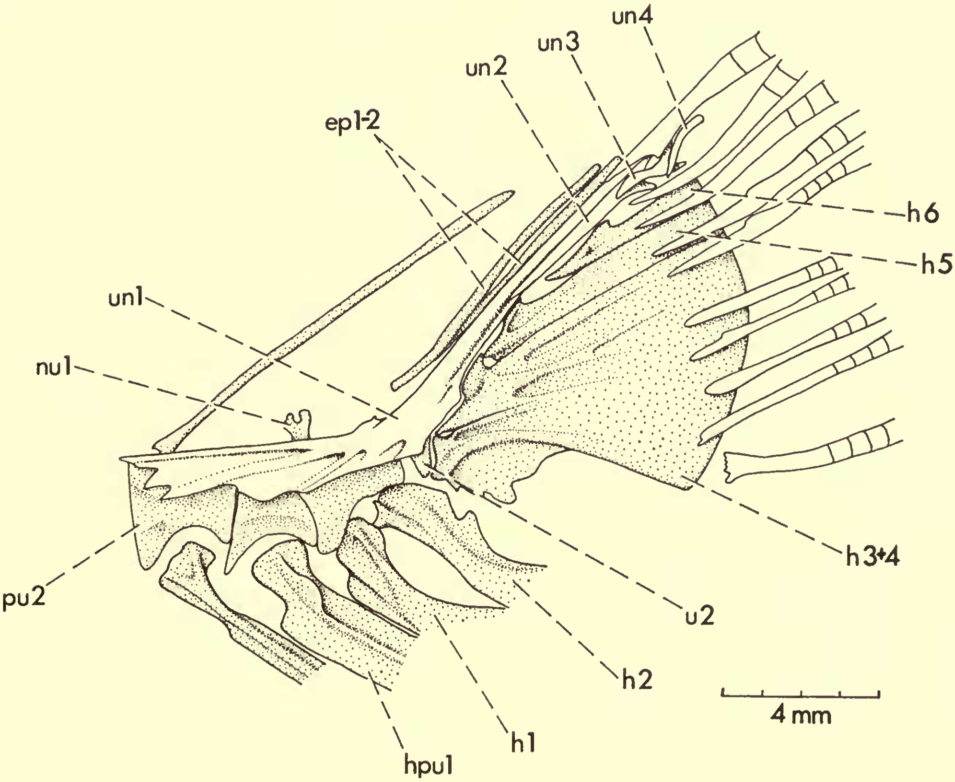
TEXT-FIG. 11. *Hiodon alosoides*, caudal skeleton of BMNH 1892.12.30.555, right side above, left side below. *ep*, epural; *h 1–7*, hypurals; *hpu 1*, haemal spine of first pre-ural vertebra; *l.nu 1*, first ural neural arch of left side; *l.un 1–3*, uroneurals of left side; *npu 1*, neural spine of first pre-ural vertebra; *pu 2*, *pu 3*, second and third pre-ural centra; *r.un. 1–4*, uroneurals of right side; *u 1*, *u 2*, first and second ural centra.

above the tip of the third uroneural (*r.un 3*). The individual abnormality on the right side of this specimen of *Hiodon alosoides* shows beyond question that uroneurals arise by modification of ural neural arches, and indicates that the morphogenetic mechanism inducing these modifications may occasionally operate beyond its usual field (the second and more posterior ural neural arches). The five uroneurals which Cavender (1966) found in some specimens of the Cretaceous *Xiphactinus*, *Ichthyodectes* and *Gillicus* may be the result of a similar modification of the first ural neural arch, for Cavender found no neural arch on the first ural centrum in these fishes, and the first uroneural in the specimen of *Ichthyodectes* which he figures (text-fig. 1A) is very like the modified first ural neural arch of *Hiodon* in size and length. This unusual plasticity of the ural neural arches in ichthyodectids and *Hiodon* (which probably belong to the same teleost lineage, Greenwood *et al.* 1966 : 360) is interesting in view of the complete loss of uroneurals in most osteoglossomorph teleosts (Greenwood 1967).

In the primitive living teleosts *Elops*, *Megalops* and *Tarpon* there are three uroneurals (Tate Regan 1910*a*, text-fig. 1; Hollister 1936, text-figs 14, 16, 19; Nybelin 1963, text-figs 4, 7, *Ur 1–3*). The first two are elongated bones ending anteriorly on the second (*Elops*) or first (*Megalops*, *Tarpon*) pre-ural and the first ural centrum respectively, the third a small splint originating well behind the second ural centrum and lying below (*Megalops*, *Tarpon*) or lateral (*Elops*) to the tip of the second. In *Elops* the anterior end of the first uroneural is forked, the upper limb passing forwards to the second pre-ural centrum, the lower ending on the first pre-ural. Tate Regan (1910*a*) considered this forking to indicate that the first uroneural is a compound bone, and saw a line of junction between the two components in some specimens. Although neither Hollister (1936) nor Nybelin (1963) saw such a line, this is probably true: in the dussumieriid *Jenkinsia* the first uroneural corresponds in position with that of *Elops* and arises as two bones which later fuse (Hollister 1936 : 279). Exactly similar forking of the first uroneural is seen in other teleosts ("*Clupavus* , Patterson 1967, text-fig. 11; *Nematonotus*, Patterson, in press, text-fig. 25) and probably always indicates that two ural neural arches have fused. Tate Regan also saw a line of junction in the second uroneural of *Elops*: if this observation were confirmed this uroneural would correspond with the compound third uroneural of normal individuals of *Hiodon* (Text-fig. 11), which it resembles in size and position, just as the compound first uroneural of *Elops* corresponds to the first two uroneurals of normal *Hiodon*, and the two large uroneurals of *Elops* would be homologous with the second to fifth ural neural arches of *Leptolepis*. The small third uroneural of *Elops*, *Megalops* and *Tarpon*, originating behind the second ural centrum, lying lateral to or behind the tip of the second (= 4th + 5th ural neural arches) and ending medial to the bases of the fin-rays, has no homologue in *Hiodon* but exactly resembles the sixth ural neural arch of *Leptolepis dubia* (*una 6*, Text-fig. 10) and a similarly placed third uroneural in many teleosts (young *Albula*, Hollister 1936, text-fig. 23; clupeoids, Hollister 1936, text-figs 43–52, Cavender 1966, text-figs 3, 4, Monod 1967, text-fig. 9, Patterson 1967*a*, text-fig. 8; salmonids, Schmalhausen 1912, pl. 18, fig. 60, Norden 1961, pls. 14, 15, Gosline 1960, text-figs 5, 12; *Argentina*, Gosline 1960, text-fig. 10; non-siluroid ostariophysans, Weitzman

1962, text-fig. 15, Gosline 1961, text-fig. 1D). Occasionally there is a second small uroneural, as in the specimen of *Salvelinus grayi* figured by Gosline (1960, text-fig. 2, UN 4). In this specimen (BMNH 1905.12.8.5) the small fourth uroneural is comparable to the seventh ural neural arch of *Leptolepis dubia* (*una* 7, Text-fig. 10), but a similar structure has not been found in other individuals of this species, or in other salmonids, although the caudal skeleton of these fishes has received more attention than that of any other group (Norden 1961, Vladykov 1962, and many ealier papers).

In a specimen of *Alepocephalus rostratus*, Gosline (1960, text-fig. 1) shows two small uroneurals (UN 2, 3) comparable with the third and fourth uroneurals in *Salvelinus grayi*, but in this specimen (BMNH 1886.8.4.7; Text-fig. 12) I find a small fourth uroneural (*un 4*) which is separate only on the left side of the fish, being fused into the third uroneural on the right side. This individual of *Alepocephalus* has three small uroneurals (*un 2–4*) comparable with the sixth to eighth ural neural arches in *Leptolepis dubia* (*una 6–8*, Text-fig. 10). The first uroneural in *Alepo-*



TEXT-FIG. 12. *Alepocephalus rostratus*, caudal skeleton of BMNH 1886.8.4.7. The neural arch of the first pre-ural centrum is broken off in this specimen. *ep 1–2*, epurals; *h 1–6*, hypurals; *hpu 1*, haemal spine of first pre-ural vertebra; *nu 1*, first ural neural arch; *pu 2*, second pre-ural centrum; *u 2*, second ural centrum; *un 1–4*, uroneurals.

cephalus (*un 1*) is very large and appears to consist of four fused ural neural arches, two ending anteriorly on the second pre-ural centrum (*pu 2*), and one ending at the hind end of both the first pre-ural and the first ural centra. This fish also has a small unmodified and paired neural arch on the first ural centrum (*nu 1*, the first ural neural arch), and an indication of the posterior end of the second ural neural arch in a process on the upper edge of the first uroneural above the hind end of the first ural centrum. *Alepocephalus* seems to exhibit the most complete set of uroneurals among living teleosts, with traces of eight ural neural arches, the first (*nu 1*) unmodified, the second to fifth much elongated and fused (*un 1*), the sixth to eighth small and separate (*un 2–4*).

Interpretation of the uroneurals of teleosts as modified ural neural arches is supported by Monod's observation (1967) that in elopoids the uroneurals may be preformed in cartilage. But it is necessary to account for two features of the uroneurals which have been taken to indicate that they are of dermal origin, the fact that they normally ossify without cartilage precursors, even in such primitive fishes as *Megalops* (Hollister 1939, text-fig. 16, Nybelin 1963 : 514) and *Clupea* (Ramanujam 1929 : 396), and the superficial appearance of the uroneurals in adult fishes, where they are usually easily differentiated from the preceding neural arches by their smooth, dense texture, suggesting dermal bone (Greenwood 1967). In pholidophorids it has been noted (p. 212) that the lateral surfaces of the ural neural arches are smooth, dense and glossy, but this is also true of the postero-dorsal processes on the heads of the upper hypurals (p. 210). The explanation of these points is probably to be found in the progressive replacement of endochondral and perichondral bone by membrane bone which occurs in the evolution of the vertebral column of teleosts. In primitive teleosts the neural and haemal arches are formed largely by ossification of cartilage, but in advanced teleosts the amount of cartilage is greatly reduced and the arches may consist entirely of membrane bone (François 1966 : 319). In *Clupea* the neural and haemal arches of the trunk ossify perichondrally and endochondrally, but the uroneurals ossify as membrane bones at a very early stage (2–2·5 cm., Ramanujam 1929 : 391). The precocious ossification of the uroneurals in ontogeny (which must occur for functional reasons) is apparently accompanied by a precocious replacement of endochondral bone by membrane bone in phylogeny, and it is this different mode of ossification which accounts for the dense texture of the uroneurals.

The history of the uroneurals in teleosts may be summarized as follows:

1. The uroneurals arose by modification of the second and more posterior members of the series of seven or eight pairs of ural neural arches present in pholidophorids, and are therefore primitively six or seven in number. Occasionally the first ural neural arch is also modified (*Leptolepis*, *Hiodon*, ? ichthyodectids).

2. There are six separate uroneurals in *Leptolepis coryphaenoides* (Text-fig. 9) and *L. normandica* (Lower Jurassic) and six or seven in *L. dubia* (Text-fig. 10), *Allothrissops* and *Thrissops* (Upper Jurassic). In post-Jurassic teleosts the number of uroneurals is reduced by loss or by fusion between members of the series.

3. The seven uroneurals of *Leptolepis dubia* are differentiated into an anterior set of four elongated, strap-like bones (representing the second to fifth ural neural arches)

and a posterior set of three short bones (ural neural arches 6–8) which originate well behind the second ural centrum and lie lateral to the anterior uroneurals. These two sets of uroneurals are recognizable in primitive members of all the major basal groups of teleosts (Elopomorpha, Clupeomorpha, Protacanthopterygii, Ostariophysi) except the Osteoglossomorpha (ichthyodectids and *Hiodon* (Text-fig. 11)), which have elongate uroneurals only: this supports the view that the Osteoglossomorpha are derived from near *Thrissops* and *Allothrissops*, in which the uroneurals are still all of one type.

4. The anterior set of four elongate uroneurals, one of which normally ends anteriorly on each of the first two pre-ural and the two ural centra, is complete only in the Cretaceous ichthyodectids (Cavender 1966) among post-Jurassic teleosts. In Upper Cretaceous " *Clupavus* " the first and second of the four are fused (Patterson 1967, text-fig. 11), in *Hiodon* the third and fourth are fused (Text-fig. 11), and in *Elops* both the first and second and the third and fourth are fused to produce two large uroneurals. Similar fusions to those in *Elops* are probably responsible for the two large uroneurals of clupeomorph, protacanthopterygian and ostariophysan fishes, and these are the only uroneurals to persist above the myctophoid level.

5. Fusions between these large anterior uroneurals and centra are common in teleosts. Usually the fusion is between the first uroneural (itself probably compound) and a compound centrum formed by fusion of the first ural and pre-ural centra: this occurs notably in clupeoids, ostariophysans, gonorynchiforms, atherinomorphs and in many paracanthopterygians and acanthopterygians.

6. A second type of fusion, especially characteristic of many protacanthopterygian and acanthopterygian groups, is the incorporation of the first ural neural arch, and usually also of the first pre-ural neural arch, into the first uroneural to produce the " stegural " of Monod (1967).

7. The posterior set of uroneurals consists primitively of three small, splint-like bones lying lateral to or behind the tip of the last elongate uroneural and ending posteriorly medial to the bases of the epaxial fin-rays. These bones represent the sixth to eighth ural neural arches of pholidophorids and *Leptolepis dubia*. Excepting *Alepocephalus* and a single specimen of *Salvelinus grayi*, I know of no post-Jurassic teleost which has more than one of these small uroneurals. *Alepocephalus* (Text-fig. 12) has three, the specimen of *Salvelinus grayi* has two. A single posterior uroneural is present in elopoids, clupeoids, many protacanthopterygians and non-siluroid ostariophysans: whether this bone is compound in origin is as yet unknown.

8. Replacement of endochondral and perichondral bone by membrane bone, which occurs in the neural and haemal arches during the evolution of teleosts, took place precociously in the uroneurals, so that they are normally ossified without cartilage precursors and differ in texture from the preceding neural arches.

(ii) *The urodermals*

In *Pholidophoropsis* and *Pholidolepis*, although the trunk scales have become thin, cycloid and have lost their enamel, there remains a small patch of thick, rhombic scales, enamelled in *Pholidophoropsis*, in the apex of the much reduced body lobe of the caudal fin (Pl. 5, fig. 2; Text-fig. 8). These scales cover the last few ural neural arches and parts of the bases of the upper hypaxial fin-rays. In *Pholidophoropsis* there are eight to ten of these scales, in *Pholidolepis* there are four. In *Leptolepis dubia* two slender, horizontally elongate bones lie one above the other lateral to the bases of the upper hypaxial fin-rays (Text-fig. 10, *ud 1–2*; Nybelin 1963, text-fig. 8, *Ur 8–9*; Patterson 1967, text-fig. 6, *D* 8–9), and two exactly similar bones are also present in *L. coryphaenoides* (32463, 32467, P.7622) and *L. normandica* (32583; Nybelin 1963, text-fig. 10, *Ur 7–8*). As Nybelin showed, since these bones are superficial to dermal fin-rays they must be dermal in origin: they are obviously homologous with the four thickened scales in this position in *Pholidolepis*, and Nybelin's term " urodermals " should be used for them. In *Leptolepis* there is no evidence of the presence of more than two urodermals. In *Allothrissops* there is normally a single urodermal (Nybelin 1963, text-fig. 11, *Ur 8*; Patterson 1967, text-fig. 3, *D* 8), but P.917*a* has two, similar in shape and position to those of *Leptolepis*. In the " *Thrissops* " specimen figured by Nybelin (1963, text-fig. 12) there are two urodermals (*Ur 14–15*), as in *Leptolepis*: in front of these, below the last elongate uroneurals, there is a row of five elongate-rhombic bones (*Ur 9–13*). These five bones do not appear to be urodermals (scales) since they are arranged in a pattern which is a dorso-ventral mirror image of the normal scale pattern on the tail (cf. text-figs. 2, 3, 15, 18 in Nybelin's paper). In *Leptolepis dubia* and *Allothrissops* I have figured a row of small bones in a similar position (Patterson 1967, text-fig. 3, D 9–11, text-fig. 6, D 10–12), but I now believe that these are postero-dorsally directed knobs on the upper hypurals, like those in pholidophorids (*p.p.h*, Text-figs 1–3, 10). The five bones in Nybelin's " *Thrissops* " specimen appear too large to be knobs on the upper hypurals and at present I am unable to interpret them. Apart from this one specimen, no Jurassic teleost is known to have more than two urodermals.

The history of the urodermals in post-Jurassic teleosts can be described briefly. The only post-Jurassic teleosts in which urodermals have been figured are the living *Elops* (Hollister 1936, text-fig. 14; Nybelin 1963, text-figs 4, 5, *Ur 4*) and Upper Cretaceous " *Clupavus* " (Patterson 1967, text-fig. 11, D6) and *Nematonotus* (Patterson, in press, text-fig. 25): in all there is only a single urodermal, lying on the fin-rays, well clear of the uroneurals. In *Elops* the single urodermal is slender and elongate, resembling those of *Leptolepis*, in " *Clupavus* " and *Nematonotus* it is shorter and more ovoid. A single ovoid urodermal also occurs in the Upper Cretaceous myctophoid *Sardinioides attenuatus* and in the living *Coregonus* and *Osmerus* (Nybelin, pers. commn) and *Argentina*. No doubt a single urodermal was present in other Cretaceous teleosts, but it will only be visible in exceptionally well preserved specimens and I have not seen one in a cursory examination of likely genera. Probably a urodermal occurs in other primitive living teleosts, perhaps in a reduced form, but again I have not found one in a brief search. In teleosts urodermals are evidently vestigial structures, retained from pholidophoroid ancestors; like other such structures (gular, pectoral and pelvic splints, caudal scutes, fringing fulcra on the upper caudal lobe, etc.), they are of limited occurrence and no obvious functional significance.

Differentiation of the scales at the tip of the reduced axial lobe of the tail from the trunk scales to produce urodermals is not confined to the pholidophoroid/teleost lineage; it also occurred in amioid holosteans (Nybelin 1963, text-figs 17–20).

(iii) *The function of the uroneurals*

It is necessary to consider why the ural neural arches should have become so remarkably modified in the evolution of teleosts. Tate Regan (1910*a*) wrote that the uroneurals " have taken on the function of strengthening the upturned vertebrae, thus replacing and inducing the abortion of the posterior centra ". Nybelin (1963) also found the uroneurals to have a strengthening function since in Jurassic forms they were best developed in fishes with a slender caudal peduncle and a large, deeply forked caudal fin. Nybelin's comparison of the uroneurals with the scale rows of the body lobe of the tail in chondrosteans is important. The scales of the caudal axis in chondrosteans are separated from those of the trunk by a more or less sharp oblique line at which the orientation of the scale rows changes from antero-dorsal–postero-ventral on the trunk to antero-ventral—postero-dorsal on the tail. That this is a real change in orientation of the scales is shown by the reversed direction of the overlapping of the scales and of the keels and peg-and-socket joints on the inner surface of the caudal scales (Schultze 1966 : 255, text-fig. 11*b*). Smith (1956 : 12) noted that this line is a functional boundary, " a hinge about which bending moments occur ". The strong fibrous attachments between the scales in each caudal scale row which Smith (1956) described in sturgeons link the rows into functional units. Smith considered the role of the caudal scale rows to be primarily protective, but it seems much more probable that they serve to stiffen the upper lobe of the tail: this may give the upper lobe less flexibility than the lower, so that the tail will generate lift even when it is externally symmetrical (Affleck 1950), as it is in *Polyodon* and many fossil chondrosteans, or it may serve simply to equalize the flexibility of the two lobes, since the lower lobe should be basically more rigid than the upper because of the direct alignment of the lepidotrichia and the supporting haemal spines. As Smith noted, the functional value of the caudal squamation in chondrosteans is indicated by the retention of these scales in many chondrosteans which have lost or greatly reduced the trunk squamation (sturgeons, *Polyodon*, *Carboveles*, *Coccolepis*, *Dorypterus*, *Birgeria*, etc.).

It is well known that the evolution of the tail in actinopterygians is linked with buoyancy and swimming efficiency (see especially Alexander 1966). The reduction in ossification and thinning of the scales characteristic of many actinopterygian lineages together with the possession of a swim-bladder lead to a reduction in specific gravity and the attainment of neutral buoyancy, which allows a great saving in energy previously expended in generating lift (Alexander 1966, table 1). In the tail the principal change involved is the gradual reduction of the body lobe of the lift-generating (epibatic, Affleck 1950) heterocercal tail towards the isobatic homocercal tail of teleosts. In pholidophorids the body lobe of the tail is greatly reduced and the fin is externally almost perfectly symmetrical (Text-fig. 7), but the endoskeleton and the arrangement of the bases of the fin-rays (Text-figs 1–4) are still strongly asymmetrical. The primitive stiffeners of the caudal axis, the scales of the body lobe, have been lost and replaced by two new sets of stiffeners, the ural neural arches (above or lateral to the notochord) and the fin-rays (below the notochord). In chondrosteans the upper hypaxial fin-rays are short, inserting on the underside of the long body lobe of the tail. In pholidophorids it appears that as the body lobe has been reduced the upper hypaxial fin-rays are elongated to retain their insertion, the long bases of these rays eventually replacing the caudal scales as stiffeners of the caudal axis. The seven or eight upper hypaxial rays of pholidophorids are very deeply cleft basally and cross the upper hypurals almost at right angles, ending on the third or fourth hypural. On the heads of most of the upper hypurals there are peg-like postero-dorsal processes which fit against the uppermost fin-ray (*p.p.h*, Text-figs 1–3) and were presumably bound to the fin-rays by connective tissue, locking them in position. This arrangement, a bundle of thin, slightly flexible rods (the bases of the fin-rays) bound to both surfaces of a row of stout rods (the hypurals) lying at right angles to them, must have been rather rigid. The ural neural arches of pholidophorids, though considerably modified (Text-fig. 5) and interlocking with each other to form a semi-rigid rod, were applied to an uncalcified notochord and did not extend forwards to gain support from the calcified part of the notochord: probably they were less effective stiffeners than the fin-ray/hypural system. It is important to note that both sets of stiffeners, the fin-rays and the ural neural arches, end at about the same level, the second ural segment (second hypural and second ural neural arch), an oblique plane of weakness which is emphasized by the termination of the first three pre-ural neural spines and the origin of the epurals in the same plane (Text-figs 1, 3, 4.). This plane of weakness corresponds with the functional boundary (hinge) at which the scales change their orientation in palaeoniscoids and at which the caudal squamation ends in such forms as *Polyodon* (Nybelin 1963, text-fig. 3), sturgeons (Smith 1956, text-fig. 1), *Birgeria* (Nielsen 1949, text-fig. 77), *Coccolepis, etc.*

In teleosts this " hinge " at the base of the upper caudal lobe has disappeared. There are two well ossified ural centra to which the uroneurals are closely applied and the uroneurals have extended forwards across the level of the " hinge " to gain support from the first two or three pre-ural centra (Text-figs 9–12), forming a highly effective set of stiffeners braced on the vertebral column. The upper principal fin-rays in Jurassic teleosts (*Leptolepis, Allothrissops, Thrissops*; Text-fig. 10; Nybelin 1963, text-figs. 8–12) have deeply cleft bases which cover the upper hypurals, as in pholidophorids, but the angle between the axes of the fin-rays and the hypurals is much smaller and the differentiation between the upper and lower principal rays in the degree of overlap on the hypurals is less: in these early teleosts the uroneurals can be seen to be replacing the fin-ray/hypural system as the main brace of the upper lobe of the tail. In Cretaceous and later teleosts the upper and lower fin-rays are normally symmetrically arranged (either both upper and lower principal fin-rays are deeply cleft at the base, as in scombrids and carangids, or neither is deeply cleft) and dorso-ventral symmetry is increased by conversion of the epaxial basal fulcra into segmented fin-rays (Tate Regan 1910*a* : 357). Even in such a primitive teleost as *Elops* the arrangement of the fin-rays shows almost perfect dorso-ventral symmetry and the upper principal rays are directly aligned with their supporting hypurals (Nybelin 1963, text-fig. 4). The uroneurals here appear to strengthen the weak supports of the upper caudal lobe (several small hypurals articulating with a small centrum or with the uncalcified notochord, Nybelin 1963, text-fig. 1) so that the two lobes of the fin will be equally flexible, and the pre-ural neural spines have increased in length, crossing the line of the " chondrostean hinge " to give added rigidity and symmetry.

These facts suggest that the tails of pholidophorids and teleosts functioned in rather different ways. In pholidophorids the body lobe is much reduced, the fin is externally symmetrical and the chondrostean system of stiffening the upper lobe by scales is obsolete, but the endoskeleton is still basically chondrostean and there was an oblique plane of weakness at the level of the second ural neural arch, both sets of stiffeners, the fin-rays and the ural neural arches, ending at this point, and the junction between the pre-ural neural spines and the epurals lying in the same plane. This plane of weakness, indicating a line of flexion, corresponds with the line of flexion in the scaling of chondrostean tails, and the musculature and mode of operation of the pholidophorid tail must have been similar to those of chondrosteans, with a stiff upper lobe swinging about an oblique axis. In teleosts, ossification of the ural and pre-ural centra and forward extension of the uroneurals have eliminated the chondrostean line of flexion. The uroneurals equalize the flexibility of the upper and lower lobes of the fin and the fin-rays lose their stiffening function and soon become symmetrically arranged. The endoskeleton is also almost symmetrical even in primitive teleosts. These changes are presumably associated with the advantages of neutral buoyancy, but it is difficult to believe that neutral buoyancy was attained only at the teleost level—a fish like *Pholidolepis* which must have had a swimbladder, had the scales reduced to the typical teleost form, and swam in sea water (specific gravity 1·025) was certainly capable of achieving neutral buoyancy. Even in *Pholidophorus*, where the scales are still thick, rhombic and enamelled, neutral buoyancy was surely attainable in view of Alexander's observation (1966 : 145) that *Lepisosteus*, with very heavily ossified scales and freshwater habitat, can remain motionless in mid-water. The advantages which the teleosts had over the pholidophorids are probably due not to the sudden acquisition of neutral buoyancy but to three factors, the advantage in the reduced rate of change of buoyancy with depth which accrues to a fish with a low specific gravity and a small swimbladder (Alexander 1966 : 148), the increased efficiency in horizontal swimming of a fish in which both lobes of the tail are equal in area and in flexibility, in which the axis is not upturned, and in which the tail swings about a vertical rather than an oblique axis (Affleck 1950), and the greater flexibility and elasticity of a trunk which contains a well ossified vertebral column and is covered by thin, flexible scales.

Returning to the question posed at the beginning of this section, why should the ural neural arches have become so remarkably modified in teleosts, I conclude that both Tate Regan and Nybelin were correct in interpreting the uroneurals as stiffeners, but that the most remarkable feature of the uroneurals, their extension forwards to articulate with or fuse with centra well in front of the segments in which they originally arose, is a method of eliminating the " chondrostean hinge ", producing a tail which swings about a vertical axis and is then free to develop internal symmetry. Tate Regan's opinion that the uroneurals " replace and induce the abortion of the posterior centra " is not strictly correct, for in phylogeny these posterior centra never existed. The uroneurals developed before the ossification of the centra, and by their presence made numerous ural centra unnecessary. In amioid holosteans, where the endoskeleton of the tail remains strongly asymmetrical, uroneurals did not develop but the " chondrostean hinge " was eliminated by the development of many ural centra extending to the tip of the notochord (Nybelin 1963, text-figs 16, 17, 19). Although amioids attained neutral buoyancy, this method of stiffening the caudal axis has prevented them from developing a fully efficient internally symmetrical tail.

(d) *Definition of the Teleostei*

In a discussion of possible taxonomic definitions of the Teleostei (Patterson 1967) I reached the conclusion that the caudal skeleton provides the most satisfactory characters for limiting the group (see also Tate Regan 1923, Gosline 1965). Under the influence of Nybelin's interpretation of the uroneurals as dermal structures (urodermals), I proposed a provisional definition of the Teleostei based on two features of caudal structure, single centrum support of the two lower hypurals, and modification of the primary squamation of the caudal axis into elongate urodermals, in contact with the vertebral column and overlain by scales. It is necessary to reconsider these criteria, since although the first remains valid the second is meaningless: it is clear that the ural neural arches of pholidophorids, which were in contact with the notochord (normally uncalcified behind the first ural centrum) and are covered by scales, are homologous with and directly comparable with the uroneurals of *Leptolepis* and teleosts. But the caudal structures of pholidophorids described in this paper have strengthened my opinion that the caudal skeleton provides the best and most practicable means of limiting the Teleostei, and that the most logical level at which to place this limit is between the pholidophorids and the leptolepids.

There are trenchant anatomical differences between the caudal skeletons of pholidophorids and leptolepids (cf. Text-figs 1–6 with Text-figs 9, 10), but the tail in leptolepids is essentially similar to those of later teleosts. These anatomical differences between pholidophorids and leptolepids appear to have important functional significance. The essential change in the tail in the pholidophorid/leptolepid transition is the elimination of the oblique line of flexion, the " chondrostean hinge ", at the base of the axial lobe of the tail, by forward extension of the uroneurals across the level of the hinge to gain support from the perichordally ossified ural and pre-ural centra. On this basis, a definition of the Teleostei can be framed as follows: " Actinopterygian fishes in which the vertebral centra are perichordally ossified, the lower lobe of the caudal fin is primitively supported by two hypurals articulating with a single centrum, and in which the ural neural arches are modified into elongate uroneurals, the anterior uroneurals extending forwards on to the pre-ural centra ".

It is worth noting that on this definition there is no evidence from the structure of the tail that the living teleosts are polyphyletic. The uroneurals of the Elopomorpha, Clupeomorpha, Protacanthopterygii and Ostariophysi appear to be based on the pattern found in *Leptolepis dubia*, those of the Osteoglossomorpha (*Hiodon* and ichthyodectids) on the pattern found in *Allothrissops*, and both these patterns can be derived from the ural neural arches of *Leptolepis coryphaenoides* and pholidophorids. Other primitive teleostean caudal characters such as nineteen principal caudal rays, two ural centra, seven hypurals, three epurals, etc., occur in basal members of all the major teleostean groups.

(e) *Taxonomy and interrelationships of Lower Liassic Pholidophoridae*

Nybelin (1966) has written preliminary diagnoses of the family Pholidophoridae *s. str.* and the genera *Pholidophorus*, *Pholidolepis* and *Pholidophoropsis*. Information on the vertebral column and caudal anatomy of these fishes allows these diagnoses to be amplified as follows:

Family ***PHOLIDOPHORIDAE*** *sensu* Nybelin (1966)

Diagnosis: See Nybelin (1966 : 425) and add " vertebral centra consisting of calcifications in the sheath of the notochord, no perichordal centra, notochordal calcifications primarily in the form of opposed dorsal and ventral hemicentra; vertebrae diplospondylous in the middle part of the caudal region; eleven or twelve hypurals, only two lower hypurals; free ventral caudal radials at the tips of the last few haemal spines and the first hypural; seven or eight pairs of ural neural arches, those behind the first or second modified into elongated splints resembling the uroneurals of teleosts; four or five epurals; the seven or eight upper principal caudal rays elongated proximally, crossing the upper hypurals."

Genus ***PHOLIDOPHORUS*** Agassiz

Diagnosis. See Nybelin (1966 : 356) and add " notochord uncalcified behind the first ural centrum, first and second ural neural arches unmodified, four epurals, twenty-two to twenty-four principal caudal fin-rays, the uppermost hypaxial fin-ray reduced."

Genus ***PHOLIDOLEPIS*** Nybelin

Diagnosis. See Nybelin (1966 : 387) and add " notochord uncalcified beyond the second ural centrum, second ural neural arch modified, four epurals, twenty to twenty-one principal caudal rays, the uppermost hypaxial fin-ray reduced, four thick, rhombic scales (urodermals) at apex of squamation of upper caudal lobe, caudal scutes small, urodermals and caudal scutes without enamel, fulcra sometimes present on lower margin of tail."

Genus ***PHOLIDOPHOROPSIS*** Nybelin

Diagnosis. See Nybelin (1966 : 411) and add "notochord calcified in the ural region, second ural neural arch unmodified, five epurals, twenty-five to twenty-seven principal caudal fin-rays, uppermost hypaxial fin-ray unreduced, eight to ten thick, rhombic scales (urodermals) at apex of squamation of upper caudal lobe, caudal scutes large, urodermals and caudal scutes enamelled."

Nybelin (1966 : 427) has also discussed the interrelationships of *Pholidophorus*, *Pholidolepis* and *Pholidophoropsis*. Mainly on the structure of the preopercular, he concluded that *Pholidolepis* is probably derived from *Pholidophorus*, from which it differs primarily in thinning of the scales and loss of enamel, and that it possibly leads on to the leptolepids. *Pholidophoropsis* he found to belong in a different pholidophorid lineage, distinct from the *Pholidophorus*/*Pholidolepis* line at least since the Upper Trias. Thinning of the scales and reduction in enamel in *Pholidophoropsis* took place independently, and this genus shows little sign of relationship to the leptolepids. Nybelin's conclusions are fully borne out by the structure of the caudal skeleton in these fishes. Of the three genera, *Pholidolepis* is closest to the leptolepids and teleosts in the number of caudal fin-rays, the number of urodermals, absence of enamel on the fin-rays, urodermals and caudal scutes, fusion of the dorsal and ventral notochordal calcifications into complete rings, modification of the second ural neural arch and tendency to lose the fringing fulcra on the lower margin of the tail. Nothing in the structure of the tail of *Pholidolepis* indicates that it was not derived from *Pholidophorus*, and the presence of four epurals and a reduced uppermost hypaxial fin-ray in the two genera suggests that they are related. *Pholidophoropsis*, although it resembles *Pholidolepis* and teleosts in the cycloid scales and the presence of urodermals, differs from *Pholidolepis* and *Pholidophorus* in the series of notochordal calcifications in the ural region and could not have evolved from *Pholidophorus* because it is more primitive in having five epurals and a higher number of principal caudal rays.

IV. SUMMARY AND CONCLUSIONS

New anatomical facts and conclusions drawn from them in this paper include the following.

1. In the Lower Liassic Pholidophoridae *Pholidophorus bechei*, *Pholidolepis* and *Pholidophoropsis* the notochord was unconstricted and centra were formed only by opposed dorsal and ventral half-ring calcifications in the sheath of the notochord. There were no perichordal centra as there are in teleosts, and in the ural region the notochord was uncalcified except in *Pholidophoropsis*. The centra were diplospondylous in the middle part of the caudal region.

2. There are eleven or twelve hypurals in these fishes, three or four more than are known to occur in teleosts, but as in teleosts there were only two lower hypurals.

3. Ventral caudal radials are present in these pholidophorids at the tips of the last three haemal spines and the first hypural. Similar elements have not been found in teleost embryos and teleosts have probably lost the ventral caudal radials, not incorporated them in the haemal spines and hypurals.

4. There are four epurals in *Pholidophorus bechei* and *Pholidolepis*, five in *Pholidophoropsis*. In teleosts there are no more than three epurals while in primitive actinopterygians there are many. The epurals are detached neural spines, serial homologues of the supraneurals above the anterior vertebrae.

5. The uroneurals of teleosts are endoskeletal structures, derived from the seven or eight pairs of ural neural arches in pholidophorids, all but the first or second of which are modified into elongate, interlocking splints resembling teleostean uroneurals. In pholidophorids and primitive teleosts the first ural neural arch normally resembles the pre-ural neural arches, but in some individuals of *Leptolepis coryphaenoides*, *Hiodon* and possibly in ichthyodectids it is modified into a uroneural. In Upper

Jurassic *Thrissops* and *Allothrissops* and in primitive Osteoglossomorpha (*Hiodon* and ichthyodectids) all the uroneurals are elongate. In the Upper Jurassic *Leptolepis dubia* and in Elopomorpha, Clupeomorpha, Protacanthopterygii and Ostariophysi the uroneurals are differentiated into an anterior set of four long bones (ural neural arches 2–5) and a posterior set of three small bones (ural neural arches 6–8). In post-Jurassic teleosts fusion and loss reduce the number of separate uroneurals. *Alepocephalus* retains the most complete set of uroneurals among living teleosts.

6. Although the Lower Liassic pholidophorids could probably achieve neutral buoyancy, their tails were still functionally heterocercal, with an axial lobe stiffened by the upper hypaxial fin-rays and the ural neural arches which swung about an oblique line of flexion at which the modified ural neural arches, the upper hypaxial fin-rays, the pre-ural neural arches and the epurals ended. This line of flexion corresponds to the " hinge " in palaeoniscoid tails at which the scale-rows change their orientation. In teleosts this " hinge " is obliterated, primarily by forward extension of the uroneurals. Teleostean uroneurals serve to equalize the flexibility of the upper and lower lobes of the tail so that it functions homocercally, and first the fin-rays and later the endoskeleton achieve dorso-ventral symmetry.

7. Precocious replacement of perichondral and endochondral bone by membrane bone accounts for the mode of ossification and " dermal " appearance of the uroneurals in teleosts.

8. In *Pholidophorus bechei* the caudal skeleton is covered by thick, rhombic enamelled scales. In *Pholidolepis* and *Pholidophoropsis* the trunk scales have lost their enamel and become thin and cycloid, but a patch of thick, rhombic scales persists at the apex of the reduced body lobe of the tail. One or two of these scales persist on the upper hypaxial fin-rays in a few primitive teleosts as urodermals. In Jurassic teleosts (*Leptolepis*, *Allothrissops*) there are one or two urodermals, in post-Jurassic teleosts no more than one is known. *Elops*, *Coregonus*, *Osmerus*, and *Argentina* are the only living teleosts known to retain a urodermal.

9. A definition of the Teleostei is proposed based on the single centrum support of the lower hypurals and the forward extension of the uroneurals on to the pre-ural centra. This definition includes the leptolepids in the Teleostei.

10. Nybelin's account of the interrelationships of the Lower Liassic pholidophorids is confirmed by caudal structure. Of the three genera dealt with here, *Pholidolepis* is closest to the teleosts.

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ADDENDUM

While this paper was in press R. Lund (1967, An analysis of the propulsive mechanisms of fishes, with reference to some fossil actinopterygians. *Ann. Carneg. Mus.*, Pittsburgh, **39**: 195–218, 12 figs.) published a discussion of the actinopterygian tail, including photographs of excellent caudal skeletons of several Jurassic genera. On questions dealt with in the present paper, the structure and nomenclature of the teleostean caudal skeleton, Lund reaches radically different conclusions from my own. Some of Lund's arguments, such as his identification of the uroneurals as intermuscular bones, are answered above, and the only points which will be mentioned here concern the nomenclature of the teleost tail. Lund rejects Nybelin's characterisation of the boundary between the ural and pre-ural regions as the point at which the caudal vessels bifurcate, writing "this point varies greatly in the teleosts" and is "modified by function". He defines hypurals as all haemal spines supporting caudal fin-rays and ural centra as all centra supporting such spines—"haemal spines that support fin-rays are *ipso facto* specialized . . . it is necessary to give these specialized haemal spines a collective name". Lund gives no evidence of variation in the point of bifurcation of the caudal vessels: my own experience and that of workers who have examined large series of teleost caudal skeletons (Goslind 1965: 191; Monod 1967: 113) is that this point is constant. And Nybelin's terminology does provide a collective name, "pre-ural haemal spines", for haemal spines supporting caudal fin-rays. The number of pre-ural haemal spines supporting fin-rays must be specified in each case simply because it varies intraspecifically (e.g. Hollister 1937, figs. 4–6; Weitzman 1962: 39).

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